Consequences of dispersal failure: kereru and large seeds in New Zealand

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A thesis submitted in fulfilment of the requirements of a Doctor of Philosophy

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University of Canterbury

2007

Kereru (*Hemiphaga novaeseelandiae*)

'What escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions' (Janzen 1974)

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Abstract

The decline of kereru (*Hemiphaga novaeseelandiae*) may limit dispersal of large-seeded plants in New Zealand, but the consequences of this are unknown.

I determined kereru disperser effectiveness by modelling seed dispersal distances (using seed retention times and movement patterns). Mean seed retention time was significantly longer for larger-seeded species, ranging from 37–181 minutes. Wild radio-tracked kereru were sedentary, remaining at one location for up to 5.25 hours. The mean flight distance was 77 m and the maximum was 1, 457 m. Estimated mean seed dispersal distances for tawa (*Beilschmiedia tawa*), puriri (*Vitex lucens*), and fivefinger (*Pseudopanax arboreus*) were 95, 98, and 61 m respectively. Kereru dispersed 66–87% of ingested seeds away from the parent tree, with 79–88% of seeds dispersed $\leq$100 m and < 1% dispersed over 1,000 m.

In a field seed-fate experiment, "pre-human" conditions (cleaned seeds, low density, away from parent, and protected from mammals) increased survival compared to "post-human" conditions (whole fruits, high density, under parent, not protected) for both taraire (*Beilschmiedia tarairi*; 15% vs. 2% survival to one year respectively) and karaka (*Corynocarpus laevigatus*; 60% vs. 11% to two years, respectively).

Fruit diameter varied considerably within karaka, taraire, and tawa, although theoretically not enough for them to be swallowed by other birds. Nevertheless, other birds are reported to occasionally take fruits of nearly all large-seeded species. Small tawa seeds produced smaller seedlings in the glasshouse; therefore selection of only smaller seeds by alternative dispersers may negatively affect tawa recruitment. Kereru are generally not gape-limited, and fruit size preferences were independent of mean fruit size.

Kereru provide effective dispersal by moving most seeds away from the parent, and enhancing seed and seedling survival. Therefore, both dispersal failure and introduced mammals negatively affect the regeneration of large-seeded trees in New Zealand.

Chapter 1. Introduction

1.1 Importance of seed dispersal

1.1.1 What is seed dispersal?

Seed dispersal is the movement of seeds away from the plant that produced them, usually referred to as the parent plant. Because adult terrestrial plants are essentially sessile, the seed is the only stage of the lifecycle during which individuals can move to another location, although genetic material is also transferred in pollen (Herrera 2002). Seeds are dispersed by both abiotic (e.g. wind, water, and gravity) and biotic mechanisms. Many plant species are dispersed by animals, either externally through attachment of seeds to fur or feathers, or internally through ingestion of fruits (Herrera 2002). Seed-eating animals such as rodents are primarily seed predators, but also disperse some seeds through incomplete recovery of seeds stored in caches (Vander Wall et al. 2005). Birds and mammals are the main seed dispersing groups, although lizards, fish, tortoises, frogs, and ants also disperse seeds in some systems (e.g. Rick & Bowman 1961; Bond & Slingsby 1984; Fialho 1990; Wenny 2000; Herrera 2002; Wotton 2002).

Internal animal seed dispersal is generally a mutualistic interaction, where plants have evolved seeds with edible pulp that are ingested by animals (Herrera 2002). The seeds are ingested incidentally by the animal disperser along with the pulp, then later defecated, regurgitated or spat out intact (Herrera 2002). Plants benefit from movement of their seeds and the animal disperser gains a food reward. Vertebrate dispersal is generally associated with large seed size, and its frequency increases with decreasing latitude, altitude, and aridity, and with increasing soil fertility (Herrera 2002). Internal seed dispersal by animals is particularly common in the wet tropics, where typically more than 70% of woody plant species have fleshy fruits (Willson et al. 1989).

The spatial distribution of seeds is fundamentally important in the ecology and evolution of plants. Seed deposition patterns can influence individual survival prospects (e.g. Howe et al. 1985; Wenny 2000), community composition (Christian 2001), gene flow and genetic structure (Gibson & Wheelwright 1995; Hamilton 1999), metapopulation dynamics (Purves & Dushoff 2005), and colonisation rates (Clark et al. 1998b). Howe & Smallwood (1982) proposed three nonexclusive benefits of seed dispersal: (1) escape from disproportionate seed or seedling mortality near the parent plant (escape hypothesis); (2)

colonisation of new habitats (colonisation hypothesis); and (3) dispersal directed to sites that enhance survival (directed dispersal hypothesis). Seed dispersal may also be advantageous for maintaining naturally or artificially fragmented metapopulations (e.g. Purves & Dushoff 2005), and ingestion of seeds by fruit-eating animals can enhance germination (Traveset & Verdú 2002).

1.1.2 Escape

Seed dispersal can enable seeds and seedlings to escape disproportionate mortality near parent plants. Some plants produce chemicals that inhibit the germination of the seeds of other species or even of their own seeds (Herrera 2002). The effects of both increasing distance from the parent and escape from high sibling densities can be advantageous. Since the greatest seed densities are typically found beneath fruiting adults, dispersal can improve survival prospects by reducing competition with conspecific seedlings (Herrera 2002). In addition, some natural enemies of seeds and seedlings respond to distance from the parent and density, thus limiting recruitment in the vicinity of conspecific adults (the Janzen-Connell model; Janzen 1970; Connell 1971).

The Janzen-Connell model proposes that distance-responsive enemies are concentrated around parent trees, resulting in higher seed/seedling mortality with increasing proximity to conspecific adults. Herbivorous insects feeding in the parent canopy, host-specific fungi, seed-predators, and soil pathogens can all act as distance-responsive enemies (Janzen 1970; Packer & Clay 2000). Connell (1971) predicted that distance effects would be stronger in seedlings than seeds, which is supported by results from a recent meta-analysis of the effect of distance from parent on seed and seedling predation (Hyatt et al. 2003). Hyatt et al. (2003) found that distance from parent generally does not affect levels of seed predation, but seedling predation tends to decrease with distance from the parent. Pathogens may provide a stronger mechanism for regulating survival near parents than predation (Packer & Clay 2000). Packer & Clay (2000) showed that *Prunus serotina* seedling mortality was greater under parent trees than away, due to higher levels of soil pathogens in the vicinity of adult plants.

Density-responsive predators concentrate their attacks on high density patches of seeds and seedlings, so that mortality increases with increasing density (Schupp 1992). An interesting example of density-dependent mortality is shown in the prairie plant *Mirabilis hirsuta*, where seed predation by ants and mice increased with increasing seed density (Platt 1976). Seedling survival was also negatively density-dependent, with survival to

maturity of around 50% at low seedling densities and virtually complete mortality at high densities (Platt 1976). Density-dependent seed predation therefore indirectly increased recruitment success by thinning seedling densities to a level where some survived (Platt 1976). Harms et al. (2000) reported negative density-dependent seedling recruitment in 53 plant species in a Panamanian forest. Nevertheless, high initial seed densities often overwhelmed density-dependent effects, so that seedling density was highest where seed density was initially greatest (Harms et al. 2000).

1.1.3 Directed dispersal

Directed seed dispersal occurs when seeds are dispersed non-randomly to sites that are suitable for establishment (Howe & Smallwood 1982). Most studies quantify seed deposition patterns by measuring dispersal distance from the parent, rather than by determining the environmental characteristics of the deposition site (Wenny 2001). As a result, directed dispersal may have been overlooked in many systems (Wenny 2001). Nevertheless, a number of examples of directed dispersal have been reported.

Some plant species absolutely require seed deposition in specific microsites or habitats in order to establish. For example, mistletoe (*Amyema quandang*) seeds must be deposited on live twigs of a specific thickness and on compatible host-trees in order to establish (Reid 1989). Mistletoe birds (*Dicaeum hirundinaceum*) were the most effective dispersers, defecating most ingested seeds on suitable-sized twigs (Reid 1989). Directed dispersal is crucial for population persistence in the columnar cactus *Neobuxbaumia tetetzon* (Godínez-Alvarez et al. 2002). The bat *Leptonycteris curasoae* deposits *N. tetetzon* seeds beneath the canopies of perennial trees and shrubs, which are the only sites where successful recruitment occurs (Godínez-Alvarez et al. 2002).

For other plant species, directed seed dispersal can enhance the probability of establishment (Fialho 1990; Wenny & Levey 1998). Fialho (1990) found that differential seed deposition patterns between lizard and frog dispersers affected germination success. Lizards tended to deposit seeds on sandy substrates in the open where few seeds germinated, while treefrogs deposited seeds in the moist interior of bromeliads where germination was enhanced (Fialho 1990). Male bellbirds in Costa Rica deposited most seeds at song perches on the edges of forest canopy gaps (Wenny & Levey 1998). Seedling survival and growth was higher at these sites than in closed forest, where fungal pathogens contributed to increased seedling mortality (Wenny & Levey 1998).

1.1.4 Colonisation

Seed dispersal also enables plants to colonise habitats that are unpredictable in space and time (Howe & Smallwood 1982). Broad dissemination of seeds may increase the likelihood of rapidly colonising newly available habitat (Howe & Smallwood 1982). Recruitment of the perennial prairie plant *M. hirsuta*, which cannot compete with other plant species in undisturbed sites, depends on successful colonisation of disturbed sites created by badger mounds (Platt 1976). Some plants species may also disperse through time by having seed dormancy, which enables establishment when suitable conditions become available.

Plants can also expand their distributional range through seed dispersal, when climatic and environmental conditions become favourable (Herrera 2002). For example, many tree species rapidly recolonised areas from which they disappeared during Pleistocene glaciations, after glacial retreat (Clark et al. 1998b).

1.1.5 Enhanced germination

Ingestion by dispersers can affect germination success by three mechanisms: (1) the scarification effect; (2) the deinhibition effect; and (3) the fertilisation effect (Traveset & Verdú 2002; Robertson et al. 2006). Seed passage through a frugivore's digestive tract may result in chemical or physical scarification of the seed coat (Traveset & Verdú 2002). Scarification may enhance germination by improving the absorption of water and gases by the seed or reduce germination if physical or chemical treatment of the seed is too vigorous (Traveset & Verdú 2002). Gut retention time may determine the degree of seed abrasion (Traveset & Verdú 2002), and for one species at least, germination success increases with decreasing seed retention time (Murray et al. 1994).

A meta-analysis of the scarification effect showed that seed ingestion by animal frugivores generally enhances germination success compared to hand-cleaned seeds (Traveset & Verdú 2002). Gut passage enhanced germination success around twice as often as germination was reduced (Traveset 1998). Seeds that absolutely require ingestion in order to germinate appear to be rare (Traveset 1998). Perhaps the only currently known example is the Galapagos tomato, which appears to require passage through the gut of the Galapagos tortoise in order to germinate (Rick & Bowman 1961). However, similar claims for other species (e.g. Temple 1977) have proved to be mistaken (Witmer & Cheke 1991). Bats and birds generally enhance germination success, while non-flying mammals and

reptiles tend to have a small positive effect and no effect on germination success respectively (Traveset & Verdú 2002).

Frugivores can also affect germination success by separating seeds from the fruit pulp and potentially removing germination inhibitors (deinhibition effect; Robertson et al. 2006). Few studies have tested for a deinhibition effect, as most experiments include only hand-cleaned seeds and ingested seeds and not whole fruits (Samuels & Levey 2005). A recent meta-analysis of 51 bird-dispersed plant species from 28 families showed that the deinhibition effect generally enhances germination and is significantly greater than the scarification effect (Robertson et al. 2006).

Seed ingestion may also enhance germination success by fertilisation of the seedling from faecal material deposited with the seed (Traveset & Verdú 2002). So far, evidence for the fertilisation effect is scarce, but Traveset et al. (2001) showed that the composition of manure deposited with seeds can affect seedling growth. However, the presence of faeces may reduce germination success in some species by promoting fungal and/or bacterial growth (Meyer & Witmer 1998).

Seeds ingested by frugivores tend to germinate faster than hand-cleaned seeds, although the difference is generally only a few days (Traveset & Verdú 2002). An increase in the speed of germination may not always be beneficial, and may even be detrimental if other factors affecting seedling recruitment favour dormancy (Traveset & Verdú 2002). It is also worth noting that both germination speed and final germination percentage are often called germination "rate" (Robertson et al. 2006), which can easily cause confusion so the latter term is thus best avoided.

1.1.6 Metapopulation maintenance

Plant metapopulations are a set of spatially separated populations linked by seed dispersal and pollination (Cain et al. 2000). Plant populations are often separated from each other by hundreds or thousands of metres, while most seeds are dispersed less than 100 m (Cain et al. 2000). The extent to which populations are linked by seed dispersal will therefore depend on the frequency of long-distance dispersal events, which are difficult to measure (Cain et al. 2000). This is a recent area of research, so to date the evidence for the role of seed dispersal in metapopulation dynamics is scarce. Nevertheless, seed dispersal is thought to play a key role in maintaining naturally patchy or human-fragmented metapopulations (Purves & Dushoff 2005).

Frugivore-generated seed deposition patterns can also influence local population genetic structure and gene flow between populations (Hamilton 1999; Jordano & Godoy 2002), which may be critical for metapopulation maintenance. However, the genetic consequences of seed dispersal are largely unknown (Herrera 2002). There is some evidence that restricted dispersal among populations leads to decreased genetic diversity, and possibly an increased risk of extinction (Shapcott 2000). *Carpentaria acuminata* is a vertebrate-dispersed palm restricted to tiny forest patches created by Pleistocene climate change in the Northern Territory of Australia (Shapcott 2000). Its seeds are dispersed by birds and flying foxes, while the flowers are visited by a wide range of animals including rodents, flying foxes, insects, and birds. Genetic diversity in *Carpentaria acuminata* populations decreases with increasing isolation, and there is significant heterogeneity and low gene flow among populations (Shapcott 2000). In some cases, fragmentation actually appears to increase gene flow among previously isolated populations, breaking down local genetic structure (Young et al. 1996).

Seed dispersal contributed a greater proportion to gene flow between *Prunus mahaleb* populations than pollen, due to the diploid nature of seeds and longer dispersal distances for seeds than pollen (García et al. 2007). While 20% of the vertebrate-dispersed seeds were from other populations, only 9.5% of the pollen (which is carried by insects) came from fathers outside the study population (García et al. 2007). Paternal genes disperse through both pollen and seed, while maternal genes disperse only in seeds (Hamilton 1999). The contribution of seed dispersal to *Prunus mahaleb* gene flow was greater than simply the proportion of immigrant seeds. Because seeds are diploid and contain genes from both parents, if all else is equal, they will contribute twice as much to the genetic breeding area of a population as pollen, which is haploid (Hamilton 1999). Hardesty et al. (2006) also showed that mean seed dispersal distances were greater than mean pollen dispersal distances, in a Panamanian tree.

1.1.7 Community structure

Seed dispersal is thought to influence community structure by establishing the spatial pattern from which communities develop. Theoretical studies show that seed dispersal could affect species coexistence through competition-dispersal trade-offs (Levine & Murrell 2003). The Janzen-Connell model (Janzen 1970; Connell 1971) proposes that seed dispersal contributes to the maintenance of high tree diversity in tropical forests. This model hypothesises that survival near parents is virtually nil (due to density- and distance-

dependent mortality), recruitment is limited to areas at some distance from conspecifics, and adults are more evenly spaced that expected from patterns of seedfall (Schupp 1992). The open spaces are therefore available for colonisation by other species, competitive exclusion is reduced, and a large number of tree species can coexist (Schupp 1992).

The efficiency of seed and seedling predators is predicted to decrease with increasing latitude, as the physical environment becomes more severe and unpredictable and affects the supply of resources (Janzen 1970). As a result, Janzen-Connell effects are expected in tropical areas but not in temperate systems (Janzen 1970). A large body of research has been devoted to testing for Janzen-Connell distance- and density-dependent effects in the tropics (e.g. Augspurger 1984; Howe et al. 1985; Schupp 1992; Hyatt et al. 2003). Although there is a paucity of studies in non-tropical areas, Janzen-Connell distance- and density-dependent effects have also been reported for temperate systems (Platt 1976; Packer & Clay 2000). Despite the prevalence of distance- and density-dependent effects (particularly for seedling recruitment), so far there is little empirical evidence to support the hypothesis that seed dispersal influences tree diversity and community structure (Levine & Murrell 2003). A recent study demonstrating increased seedling diversity due to negative density-dependent recruitment provides some support for the hypothesis (Harms et al. 2000).

1.2 Seed dispersal in New Zealand

1.2.1 Plant dispersal modes

The proportion of trees in the New Zealand flora with fleshy fruits that rely on animals for dispersal is unusually high (around 70%) compared to other temperate floras (Burrows 1994a). This may be due to the taxonomic affinities of many New Zealand trees to tropical species (Burrows 1994a). The proportion of woody plant species including shrubs and of all plant species with fleshy fruits are both comparable to other temperate areas (48% and 12% respectively) (Burrows 1994a; Lord et al. 2002). The proportion of New Zealand tree species with wind-dispersed seeds is correspondingly low (5.5%), but is higher for all woody species (43.5%; Burrows 1994a).

1.2.2 New Zealand frugivores

New Zealand has a limited range of vertebrates available to disperse seeds compared to other regions. Until recently, the only terrestrial mammals known to have occurred in New Zealand were bats (Lloyd 2001). Fossil remains of a mouse-size mammal from the Miocene (19–16 Ma) were discovered recently, although little is known of its past ecological role (Worthy et al. 2006). The native New Zealand terrestrial vertebrate fauna is dominated by birds and lizards (Towns & Daugherty 1994; Bunce et al. 2003).

The arrival of humans has had a devastating impact on the native New Zealand fauna. Introduced mammalian predators, habitat loss, and hunting have caused the extinction of numerous endemic vertebrate species and the decline of many others, including bats (Lloyd 2001), reptiles (Towns & Daugherty 1994), and birds (Holdaway et al. 2001). Of the three bats species that existed in New Zealand, the two Microchiropteran bat species (the lesser short-tailed bat *Mystacina tuberculata* and the greater short-tailed bat *M. robusta*) probably both dispersed some seeds (Lord et al. 2002). The greater short-tailed bat is now extinct, while the lesser short-tailed bat is highly threatened and plays a limited role in dispersal of small-seeded species (Lord *et al.* 2002).

Introduced mammals have had a devastating effect on the lizard fauna in New Zealand, with 40% of lizard species driven to extinction in the last millennium (Towns & Daugherty 1994). Many remaining lizard species have been eliminated from vast areas of their previous ranges, with 41% now confined almost entirely to rat-free offshore islands (Towns & Daugherty 1994). The density of more widespread lizard species has declined

drastically (Whitaker 1987). Lizards disperse small fleshy fruits in New Zealand and probably played a greater role in pre-human times when lizards were more abundant and widespread (Whitaker 1987; Wotton 2002). Nevertheless, most fleshy-fruited species in New Zealand have probably always been bird-dispersed (Clout & Hay 1989).

Recent evidence indicates that invertebrate weta (Orthoptera), many of which are threatened with extinction by introduced mammals, may provide limited dispersal of fleshy-fruited species with small seeds (Burns 2006; Duthie et al. 2006). However, weta destroyed many of the seeds ingested, and ingested only the fruit pulp for other species, so their role as effective seed dispersers remains uncertain (Burns 2006; Duthie et al. 2006).

Clout & Hay (1989) listed three groups of extinct birds that ate some fruit: moa (*Dinornithidae*), huia (*Heteralocha acutirostris*), and piopio (*Turnagra capensis*). Ten moa species are recognized currently (Bunce et al. 2003), a number of which included fruit in their diet (Burrows et al. 1981). It is difficult to assess the role of extinct moa species as seed dispersers, as only limited information is available. Only the two species of giant moa (*Dinornis novaezealandiae* and *D. robustus*) are known to have fed under forest canopies and included fruits in their diet (Worthy & Holdaway 2001). The little bush moa (*Anomalopteryx didiformis*) lived in forest habitats but fed outside the forest canopy (R. N. Holdaway personal communication). Giant moa carried large quantities of gizzard stones in their gut, which would have destroyed seeds with thin seed coats, although woody seeds may have passed intact (Clout & Hay 1989). Other moa species probably played a seed dispersal role in non-forested habitats, particularly for divaricate species.

Other frugivorous bird species that were previously widespread, such as kokako (*Callaeas cinerea*), stitchbird (*Notiomystis cincta*), and saddleback (*Philesturnus carunculatus*), are now confined to predator-free offshore islands or intensively managed mainland sites. Many of the remaining avian frugivores which are still widespread, including kereru (the New Zealand pigeon, or kukupa; *Hemiphaga novaeseelandiae*, Columbidae) and tui (*Prosthemadera novaeseelandiae*), have decreased in abundance and disappeared from some areas (Pierce et al. 1993; Higgins et al. 2001).

1.2.3 Dispersal of large-seeded species

Gape size tends to limit the size of fruits an animal can swallow, particularly in birds (Wheelwright 1985). The maximum transverse diameter of fruits, rather than the length, restricts which species and individuals can swallow fruits (Mazer & Wheelwright 1993). Frugivores can avoid gape limitation to some extent by eating small-seeded fruits in pieces,

and by squashing fruits in their bill prior to swallowing (Levey 1987). Nevertheless, fewer animal species are capable of dispersing the seeds of large-seeded species, which consequently are more vulnerable to dispersal failure. Human activities are also more likely to reduce populations of large-bodied vertebrates and drive them to extinction (Brook & Bowman 2004).

For large-seeded tree species with fruits greater than 14 mm in diameter, the kereru is the only known extant frugivore with a gape large enough to swallow fruits and disperse the seeds (McEwen 1978; Clout & Hay 1989). The five widely recognised large-seeded tree species in New Zealand are tawa (*Beilschmiedia tawa*, Lauraceae), taraire (*B. tarairi*), puriri (*Vitex lucens*, Verbenaceae), karaka (*Corynocarpus laevigatus*, Corynocarpaceae), and tawapou (*Planchonella costata*, Sapotaceae). Although tawaroa (*B. tawaroa*) is also listed by Clout & Hay (1989), I follow the taxonomy of Allan (1961), which includes *B. tawaroa* within *B. tawa*.

Some ground cover species also have large single-seeded fruits, including *Colensoa physaloides* (fruits 10–25 mm diameter) and *Libertia ixiodes* (15–20 mm) (Dijkgraaf 2002). Dijkgraaf (2002) suggests that these lower stature species could have been dispersed by several species, including moa. However, moa and many other ground-dwelling bird species are extinct and the current dispersers for these plant species are unknown. Kereru probably spent more time foraging on the ground prior to the introduction of predatory mammals. Some native species modify their behaviour in the presence of introduced mammals. For example, tree weta (*Hemideina crassidens*) occupy galleries closer to the ground when mammalian predators are absent (Rufaut & Gibbs 2003), and kereru forage extensively on the ground on predator-free Kapiti Island (DMW personal observation) and also on Little Barrier Island (D. Kelly, personal communication). These large-seeded fruits may have been dispersed by kereru along with other ground-dwelling birds.

Kereru

Kereru are large-bodied (c. 650g; Clout & Tilley 1992), frugivorous pigeons endemic to New Zealand (Clout & Hay 1989). The kereru plays an important seed dispersal role, consuming fruits of at least 70 plant species and defecating the seeds intact (McEwen 1978; Clout & Hay 1989). While still widespread throughout New Zealand, kereru numbers have declined due to introduced predators, habitat loss, and hunting (Clout et al. 1995b). The inherently low reproduction rate of kereru (a single egg per clutch, maximum

of 2–3 clutches per year (Heather & Robertson 2000), and no nesting attempted in low-fruit years (Clout et al. 1995b)) is exacerbated by high levels of predation by stoats (*Mustela erminea*), rats (*Rattus rattus*), possums (*Trichosurus vulpecula*), and cats (*Felis catus*) (Clout et al. 1995b; Pierce & Graham 1995; Innes et al. 2004). Possums and rats also compete with kereru for food, eating ripe and unripe fruits in the canopy (Dijkgraaf 2002). Despite the legal protection of kereru since 1921, illegal hunting continues to occur, particularly in Northland (Pierce et al. 1993; Clout et al. 1995b; Pierce & Graham 1995).

Kereru (New Zealand pigeon, *Hemiphaga novaeseelandiae*)

1.3 Thesis outline

The main objectives of this thesis were to determine the effectiveness of kereru as seed dispersers and to determine their importance for dispersal of large-seeded tree species. I addressed some fundamental questions relating to the effectiveness of kereru as seed dispersers in Chapters 2, 3 and 4. Seed disperser effectiveness is defined as the contribution a disperser makes to a plant's future reproduction, and has both quantitative and qualitative components (Schupp 1993). Seed dispersal quantity depends on the number of visits a disperser makes, and the number of seeds dispersed per visit. Dispersal quality depends on the treatment of seeds in the disperser's mouth and gut, and seed deposition patterns (Schupp 1993). Dispersal distance is a key component of the spatial pattern of

seed dispersal, but is very difficult to measure. I therefore used a modelling approach to estimate kereru seed dispersal distances, combining data on seed retention times (Chapter 2) and kereru daily movement patterns (Chapter 3). In Chapter 4, I tested the effect of kereru gut passage on seed germination in a large-seeded tree.

A decline in, or loss of, frugivorous animal populations can disrupt seed dispersal mutualisms (Bond & Slingsby 1984; Chapman & Chapman 1995; Traveset 1995; McConkey & Drake 2002). However, few studies have established that the loss of a single species of seed disperser leads to failure of plants to disperse any seeds ("dispersal failure"; Bond & Slingsby 1984). Even fewer have demonstrated significant consequences of seed dispersal failure for plant populations or communities (Christian 2001). The concept of dispersal failure is discussed in more detail in the introduction and discussion of Chapter 5. Although the disappearance of kereru from New Zealand forests is predicted to have serious consequences for the regeneration of large-seeded trees (McEwen 1978; Clout & Hay 1989), this hypothesis has not been tested. To test the effect of dispersal failure on early recruitment in large-seeded species, I compared the fate of dispersed and undispersed seeds in a field experiment (Chapter 5).

Finally, I investigated some evolutionary aspects of seed dispersal by potential replacement dispersers of large-seeded trees (Chapter 6) and by kereru (Chapter 7). Seed size can vary considerably within a plant species (Michaels et al. 1988) and can influence the probability of survival and establishment (Moles & Westoby 2004). Gape size tends to limit the size of fruits that animals can ingest, which could result in non-random removal by fruit size and have important implications for plant fitness (Wheelwright 1985). For further discussion of this topic see Chapters 6 and 7. Research in Chapter 7 was conducted in collaboration with Jenny Ladley and has been accepted for publication (Wotton & Ladley in press). I conclude by synthesising my research results with existing information to assess the importance of kereru as dispersers of large-seeded tree species in New Zealand (Chapter 8).

Chapter 2. Kereru seed retention times[1]

The hazards of fieldwork! A captive kereru investigating Jenny Ladley's jacket.

2.1 Abstract

I offered ripe fruits of tawa (*Beilschmiedia tawa*), taraire (*B. tarairi*), and puriri (*Vitex lucens*) to captive kereru (New Zealand pigeons, *Hemiphaga novaeseelandiae*) and recorded seed retention times. I also recorded seed retention times while radio-tracking wild kereru in Taranaki and Canterbury. I report wild kereru retention times for tawa, puriri, miro (*Prumnopitys ferruginea*), fivefinger (*Pseudopanax arboreus*), and kahikatea (*Dacrycarpus dacrydioides*) seeds. Where data were available for the same plant species from wild and captive kereru, retention times were similar. Seed retention time differed significantly among fruit species and was positively related to seed mass. Mean retention times ranged from 37–45 minutes for the two smallest-seeded species (fivefinger and kahikatea) up to 109–181 minutes for the three largest species (puriri, taraire, and tawa). I also report the second published instance of regurgitation by kereru.

[1] A revised version of this chapter has been accepted for publication (Wotton et al. in press).

2.2 Introduction

Internal transport of fleshy fruits by avian frugivores is a widespread seed dispersal mechanism. Frugivorous birds and fruiting plants both encounter a range of trade-offs relating to the length of time dispersers retain seeds after ingesting fruits. The treatment of seeds by animal dispersers can have importance consequences for plant reproductive success. From the plant's perspective, seed retention time is a trade-off between dispersal distance and seed viability (Murray et al. 1994). Longer seed retention times generally result in greater dispersal distances (Murray et al. 1994; Holbrook & Smith 2000), but decreased seed viability (Murphy et al. 1993; Murray et al. 1994; Charalambidou et al. 2003). For animal frugivores, seed retention time is a trade-off between absorbing nutrients from the fruit pulp and eliminating the indigestible seed 'ballast' (Snow 1971; Levey & Grajal 1991). The presence of seeds in a bird's gut limits its capacity for food ingestion (Sorensen 1984). In addition, the weight of seeds increases the energy expenditure required for flight (Levey & Grajal 1991). However, some plants appear to have the ability to influence gut passage times, which consequently may not always be under the bird's control (Murray et al. 1994; Levey et al. 2007).

In the New Zealand flora around 70% of trees, 48% of woody plants (Burrows 1994a), and 12% of all plant species (Lord *et al.* 2002) have fleshy fruits that rely on animals for dispersal. The only terrestrial mammals in New Zealand are two threatened species of Microchiropteran bat, one of which eats some fruit and may play a limited role in dispersal of small-seeded species (Lord *et al.* 2002). Lizards disperse small fleshy fruits in New Zealand (Whitaker 1987; Wotton 2002), but most fleshy-fruited species are bird-dispersed. Kereru (the New Zealand pigeon, *Hemiphaga novaeseelandiae*) are large (c. 650g; Clout & Tilley 1992), frugivorous pigeons widespread throughout New Zealand (Clout & Hay 1989). Kereru play an important seed dispersal role, consuming fruits of at least 70 plant species and defecating the seeds intact (McEwen 1978; Clout & Hay 1989). The only published kereru seed retention times are for miro (*Prumnopitys ferruginea*, Podocarpaceae) (Clout & Tilley 1992). My research aimed to answer the following questions:

1) How long does it take for seeds of a range of native species to pass through the gut of kereru?

2) Do kereru seed retention times vary among plant species?

3) Is seed retention time related to seed size?

2.3 Methods

2.3.1 Study sites

I conducted seed passage trials with captive kereru in outdoor aviaries at Orana Wildlife Park and Willowbank Wildlife Reserve, in Christchurch, New Zealand. The aviaries were generally large enough for kereru to undertake short flights, with the exception of one injured individual, which was unable to fly and was held separately in a smaller aviary. Captive kereru were maintained on a diet of sweet corn, peas, commercially available fruit (e.g. kiwifruit), bread, and seeds. Maintenance food for kereru was placed in the aviaries once a day, usually around mid morning.

I radio-tracked wild kereru in Taranaki and on Banks Peninsula, Canterbury, New Zealand, which had been radio-tagged for other studies (R.G. Powlesland personal communication; Campbell 2006). Kereru in Taranaki were located in and around New Plymouth city (39° 04′ S 174° 05′ E) in native forest remnants and in urban parks with mixed native and introduced vegetation. On Banks Peninsula, kereru were mostly tracked in Hinewai Reserve (43° 49′ 37 S 173° 02′ 42″ E) and on adjacent farmland. One individual was tracked in the nearby township of Akaroa (43° 48′ 24″ S 172° 58′ 26″ E).

2.3.2 Captive trials

I offered captive kereru native fruits of three species: tawa (*Beilschmiedia tawa* (A.Cunn.) Benth. et Hook.f. ex Kirk, Lauraceae), taraire (*B. tarairi* (A.Cunn.) Benth. et Hook.f. ex Kirk), and puriri (*Vitex lucens* Kirk, Verbenaceae), all of which are important in the diet of wild kereru (McEwen 1978). Both tawa and taraire have large, dark purple to black fleshy fruits with a single seed. Tawa fruits are approximately 27 x 16 mm (length x diameter) (Wotton & Ladley in press). Taraire fruits are larger than tawa, measuring approximately 32 x 19 mm (Wotton & Ladley in press). Puriri has pinkish-red, fleshy fruits measuring 18 x 16 mm (J. M. Lord, personal communication). The dispersal unit of puriri (for convenience hereafter referred to as a seed) consists of between one to four seeds enclosed in a woody endocarp (Godley 1971), which remains intact after ingestion (Webb & Simpson 2001). Taraire and puriri fruits were collected from Wenderholm Regional Park (36° 32′ 15″ S 174° 42′ 24″ E), near Auckland, New Zealand, and tawa fruits were collected from Blue Duck Reserve, Kaikoura, New Zealand (42° 14′ 10″ S 173° 46′ 59″ E).

I offered fruits of a single species in separate trials once or twice to each individual kereru. Fruits were offered to ten kereru in total, although only five birds actually ingested

fruits. Twenty fruits of a single species were placed in the usual feeding tray in the aviary in the morning prior to normal food being made available. I recorded the times at which fruits were eaten and the number of fruits eaten. Any fruits not consumed within 10 minutes of the first fruit being swallowed were removed, and the normal food supply was placed in the feeding tray. I observed kereru continuously until all seeds were recovered, recording the time of each defecation and the number of seeds defecated. I use the term 'seed retention' to encompass both seeds that were defecated and those that were regurgitated. 'Seed passage' refers to only those seeds that were defecated. I calculated seed retention times by subtracting the midpoint of the time between ingestion of the first and last fruits from the time of egestion.

2.3.3 Wild seed passage times

I collected data on seed passage times while radio-tracking wild kereru from January to April 2006. Kereru were fitted with Sirtrack radio-transmitters and located using Sirtrack TR4 and R1000 receivers and 160MHz folding Yagi antennae. I tracked individual kereru continuously from early morning for up to 8.5 hours. During each tracking session I recorded the time of feeding observations, noting the species of any fruit consumed. I also recorded the time of any defecations containing seeds, and when these could be collected identified the seeds to species. I determined seed passage times only for those observations that met the following criteria: (1) kereru defecated seeds after the first observation feeding on a fruit species for that day and prior to repeated feeding on the same species; or (2) there was a minimum five hour interval between the feeding observation and any prior ingestion of fruit of the same species, and no repeated feeding was observed on the same species prior to seed defecation. I calculated seed passage times by subtracting the time at the midpoint of the feeding bout from the time of defecation.

2.3.4 Data analysis

For captive trials I tested for differences in seed retention time between fruit species using a two-tailed ANOVA. Where sample size was sufficient I tested differences within fruit species between wild versus captive kereru using a two sample t-test. For fruit species where I had both wild and captive retention times I combined all data for that plant to calculate an overall mean seed retention time, which was used in subsequent analyses. I used a two-tailed ANOVA to test for differences in seed retention time between fruit species (wild and captive data combined). I carried out a linear regression to determine

whether mean seed retention time was related to mean seed mass across all plant species. I included captive kereru passage time data for miro seeds from Clout & Tilley (1992) in this analysis. Air-dried seed mass data were obtained from Moles et al. (2000) for all species except tawa and taraire, for which I collected data from the site at which fruits fed to captive kereru were collected. I included seeds that were regurgitated in all analyses as there did not appear to be any consistent effect of seed treatment on seed retention time, although the number of observations was too small to test this. All analyses were carried out using R version 2.1.1 (R Development Core Team 2005).

2.4 Results

2.4.1 Captive trials

Captive kereru were unfamiliar with native fruits, often dropping fruits repeatedly while attempting to swallow them. The five kereru that did not ingest any fruits made no attempt to swallow them, showing little interest in the fruits. Tawa fruits were readily ingested by five kereru, although retention times were recorded for only four individuals. Only two kereru swallowed puriri and taraire fruits; individuals that had eaten tawa fruits in previous trials made no attempt to swallow either of these species. With practice, kereru appeared to be able to manipulate the elliptical tawa fruits more easily than those of puriri (which are almost spherical), despite the fact that tawa fruits are considerably larger. Kereru manoeuvred tawa fruits lengthwise in their bill prior to swallowing. Kereru appeared to experience considerable difficulty swallowing taraire fruits due to their large diameter. Nevertheless, in the wild kereru are often observed feeding on taraire fruits.

The number of fruits ingested during a feeding bout appears to be limited by both fruit size and the size of the kereru's crop. In a single feeding bout captive kereru nearly always ingested six or seven puriri fruits, four tawa fruits, or one taraire fruit (from smallest to largest fruits respectively). Kereru defecations contained a single seed of tawa or taraire, or between one and three puriri seeds.

Seed retention times varied significantly among plant species within captive trials (Table 2.1). Captive kereru retention times ranged from a minimum of 43 minutes for a puriri seed to a maximum of five and a half hours for the slowest tawa seed (Table 2.2).

Table 2.1. Results of two-tailed ANOVA testing for differences in mean seed retention time among fruit species ingested by kereru.

Source	df	SS	MS	F	P
Captive kereru					
Fruit species	2	57193	28597	4.952	0.014
Residuals	30	173236	5775		
Captive and wild data combined					
Fruit species	5	161483	32297	7.1751	< 0.0001
Residuals	58	261071	4501		

Table 2.2 Seed retention times for native fruits swallowed by captive and wild kereru. All times are in minutes.

Plant species	Common name	Mean	SD	Range	Sample sizes (seeds, defecations, birds)
Captive					
Beilschmiedia tawa	tawa	180.8	100.3	57–330	15, 13, 4
B. taraire	taraire	137.8	55.3	74–192	4, 4, 2
Vitex lucens	puriri	91.9	42.3	43–189	14, 11, 2
Wild					
Beilschmiedia tawa	tawa	254.0	11.3	246–262	2, 2, 1
Dacrycarpus dacrydioides	kahikatea	44.5	2.1	43–46	-, 2, 1
Prumnopitys ferruginea	miro	80.0	-	80–80	1, 1, 1
Pseudopanax arboreus	fivefinger	37.4	9.9	19–50	-, 9, 1
Vitex lucens	puriri	122.4	66.3	63–269	17, 10, 3

I observed two kereru regurgitate seeds and fruits during captive feeding trials. The first bird ingested four tawa fruits during a single feeding bout and all four seeds were regurgitated in two events. The first regurgitation occurred 57 minutes after ingestion, during which the kereru ejected one intact fruit and one seed with the pulp partly digested. During the second event (5 ½ hours after ingestion), the kereru regurgitated the other two seeds with the pulp completely digested. The same individual also regurgitated a taraire seed with the pulp partly digested 110 minutes after ingestion. The second kereru regurgitated an intact taraire fruit 74 minutes after swallowing it.

2.4.2 Wild seed passage times

I collected wild seed passage times for five plant species (Table 2.2, Figure 2.1), two of which were also used in captive trials in this study. The number of seeds contained in wild kereru defecations varied from one seed for tawa, or 1–3 puriri seeds, to more than ten seeds of fivefinger (*Pseudopanax arboreus*) or kahikatea (*Dacrycarpus dacrydioides*). A single miro seed was collected from a dropping that also contained one puriri seed. Seed retention times for fivefinger and kahikatea are for defecations rather than individual seeds. Due to the small seed size for these two species I was unable to recover and count all seeds. Although I recorded wild passage times for only a small number of seeds, these were consistent with times recorded for captive kereru (Table 2.2, Figure 2.1). T-test results showed that puriri retention times did not differ significantly among captive and wild kereru (means of 92 and 122 minutes respectively, d.f. = 29, t = -1.487, P = 0.148). The seed passage time of 80 minutes I recorded for a single miro seed in the wild was also comparable to the mean for captive birds of 95.4 minutes (Clout & Tilley 1992). Similarly, the two tawa seed passage times I collected from wild birds were within the range I recorded for captive birds (Table 2.2).

2.4.3 Differences among species

The overall mean seed retention time for kereru was 120 ± 82 minutes. Mean seed retention time, combining captive and wild data, was 108.6 ± 57.9 minutes for puriri and 189.4 ± 97.0 minutes for tawa. Seed retention time differed significantly among fruit species (Table 2.1) and was significantly affected by seed mass (Figure 2.2).

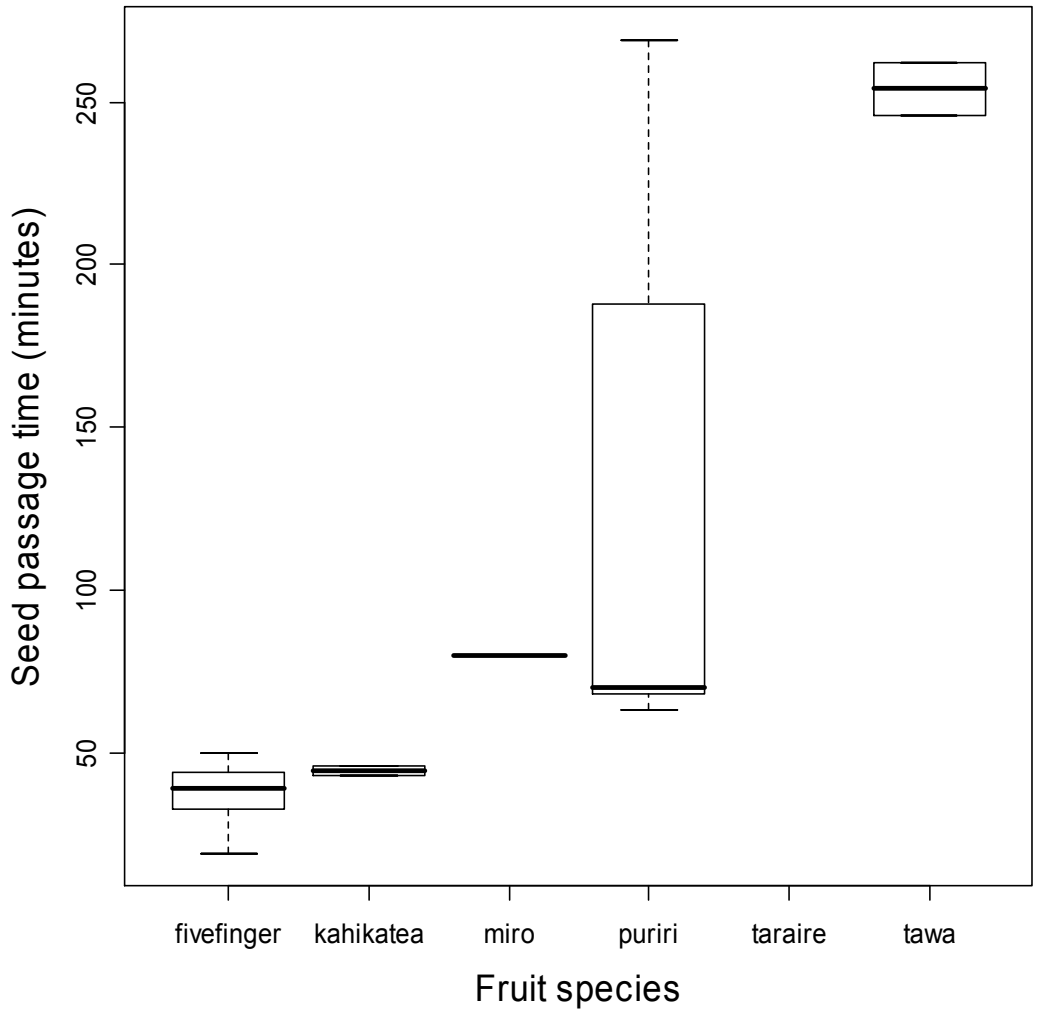


Figure 2.1 Seed passage times for native fruits ingested by wild kereru. Horizontal lines within boxes indicate the median, and lower and upper sides of boxes represent the 25th and 75th percentiles respectively. Error bars show 1.5 times the interquartile range of the data.

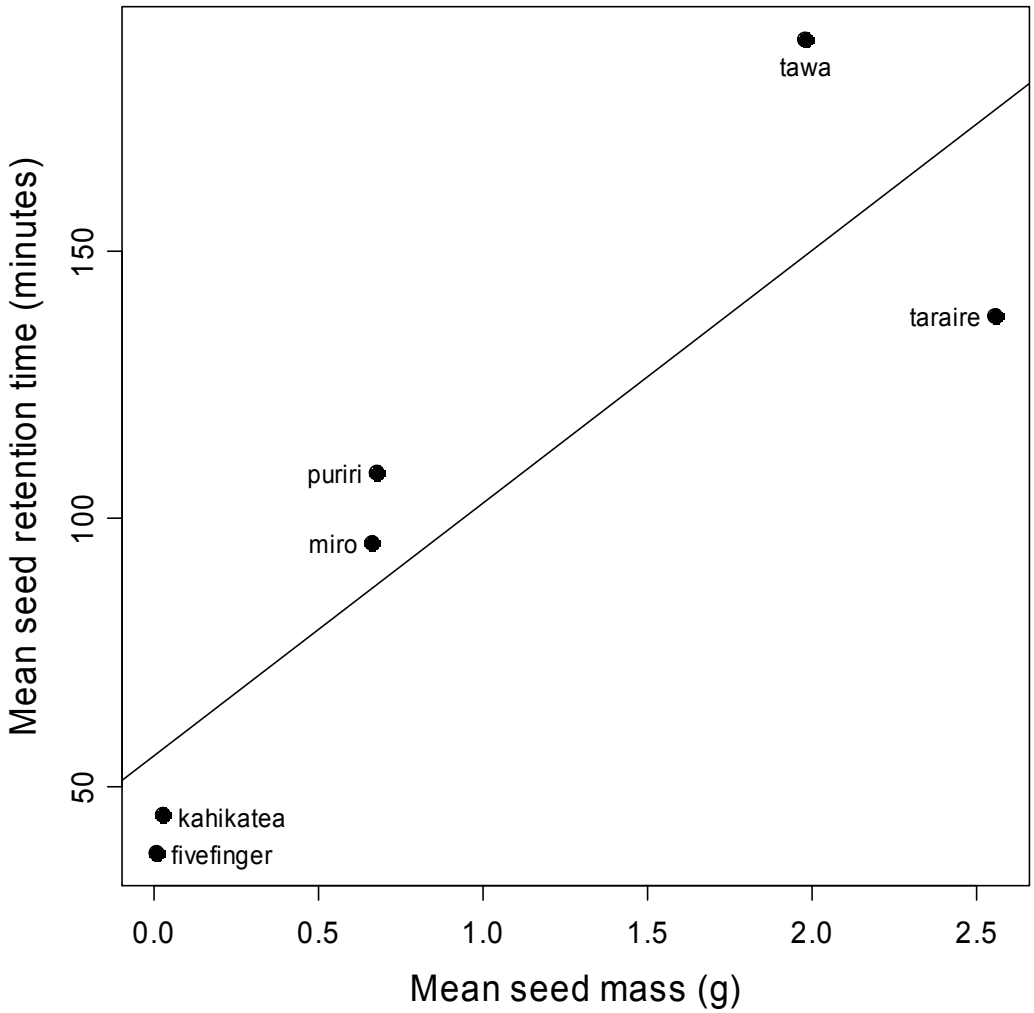


Figure 2.2 Relationship between mean seed mass and mean seed retention time for six fruit species consumed by wild and captive kereru. Seed mass data are from Moles *et al.* (2000), except for tawa and taraire measured at my sites. The relationship was significant (adjusted $R^2 = 0.687$, regression equation = 55.61 + 47.22x, F = 11.96, d.f. = 1 and 4, P = 0.026).

2.5 Discussion

Kereru seed retention times are relatively long compared to other avian frugivores. Small passerines typically defecate seeds within an hour of ingestion (Sorensen 1984; Murphy et al. 1993), and often within 20 minutes (Levey 1987; French 1996). This contrasts with kereru seed retention times, which range from 19 to 330 minutes, with an overall mean of two hours. However, given the large size of kereru my results are consistent with evidence that seed retention time increases with frugivore body size (Herrera 1984; Levey 1986; Holbrook & Smith 2000).

The relationship between seed passage time and seed size appears to be inconsistent among avian seed dispersers. Seed passage time in kereru increases with increasing seed size, which agrees with results reported for a number of other studies (Sorensen 1984; Holbrook & Smith 2000; Westcott et al. 2005). However, other authors show either a negative relationship (Levey 1986; Levey & Grajal 1991; Stanley & Lill 2002; Fukui 2003), or no relationship between seed passage time and seed size (Sun et al. 1997). It appears that other characteristics of both fruits and dispersers also influence seed passage time. For example some birds may process carbohydrate-rich foods more rapidly than lipid-rich ones (Afik & Karasov 1995). Lipids require more time to digest and absorb than simple sugars (Witmer & Van Soest 1998). Specialist frugivores can also have a more rapid gut passage rate than fruit- or seed-predators and non-frugivores (Herrera 1984).

Frugivores face conflicting demands between retaining fruits for a sufficient period of time to assimilate nutrients and discarding the indigestible seed as rapidly as possible (Murray et al. 1994). Regurgitation is a common method of rapidly processing large seeds, where birds regurgitate large seeds and defecate smaller ones (Johnson et al. 1985; Levey 1986, 1987; McConkey et al. 2004). Nevertheless, I know of only two previously published records of regurgitation in New Zealand, by a single kereru that regurgitated a puriri fruit (Simpson 1971) and by South Island robins (Powlesland 1979). *Hemiphaga chathamensis* was also observed regurgitating *Myrsine chathamica* fruits on Chatham Island, New Zealand (R.G. Powlesland personal communication).

Regurgitation may be under-reported as it is difficult to observe in dense forest where kereru are often found. However, kereru do not appear to use regurgitation as a means of eliminating large seeds rapidly. Regurgitation events I observed did not appear to decrease seed retention time; in fact the longest retention time recorded was for two

regurgitated tawa seeds. Captive kereru that regurgitated seeds or fruits failed to fully process the pulp for four of the six fruits, and whole fruits were regurgitated in both wild events. Kereru appear to obtain little benefit from regurgitation in terms of rapid seed processing or nutrient assimilation, and may regurgitate fruits only when they are under stress or have eaten a large amount (McEwen 1978).

Plants also experience costs and benefits related to seed retention time. As seed retention time increases, dispersal distances become greater (Murray et al. 1994; Holbrook & Smith 2000), which is generally advantageous to the plant. Long-distance dispersal enables plants to colonise new sites (Howe & Smallwood 1982) and maintain metapopulations in naturally or artificially fragmented landscapes (Cain et al. 2000). On the other hand, longer seed retention times decrease the number of fruits dispersed, since frugivore ingestion is limited by gut capacity (Sorensen 1984; Levey 1986; Levey & Grajal 1991). Increasing seed retention time can also decrease germination success (Murphy et al. 1993; Murray et al. 1994; Charalambidou et al. 2003).

Seed passage trials conducted with captive birds have a number of potential limitations (Holbrook & Smith 2000). Captive birds are likely to be relatively inactive compared to wild ones and seed passage times may therefore be slower. However, feeding by kereru in the wild is often followed by a long period of inactivity, sometimes lasting for over 5 hrs (McEwen 1978; Chapter 3). Indeed, Levey & Grajal (1991) note that "Many fruit-eating birds and bats are inactive for long periods after a meal".

In addition, the diet of captive birds may differ considerably to that of wild birds. Individual birds in captivity can modify their gut processing rate in response to changes in diet (Afik & Karasov 1995). The captive diet of kereru I used differed from that of wild kereru, although it did include fruit. Offering kereru only a single fruit species during feeding trials may also have influenced gut passage rates. However, kereru often feed on only one fruit species during a feeding bout (Clout & Hay 1989). McEwen (1978) examined the stomach contents of 177 kereru and found that fruit usually consisted of only a single plant species. I have shown that seed retention times were similar for wild and captive birds. Wild-bird seed retention times are difficult to measure and there are only a few previously published estimates (Howe 1977; Howe & Vande Kerckhove 1981; Wheelwright 1991). Only one of these actually quantified seed retention times for wild birds (Wheelwright 1991).

Seed dispersal distance is a function of frugivore movement patterns and seed retention times (Westcott et al. 2005). My results will enable estimation of seed dispersal

distances by kereru for a range of plant species. Seed retention times of up to five and a half hours combined with seasonal movements of tens of kilometres (Clout et al. 1986; Clout et al. 1991) indicate the potential for effective seed dispersal over long distances by kereru.

Chapter 3. Modelling kereru seed dispersal distances

Maggie Tisch radio-tracking kereru at Lake Mangamahoe, Taranaki

3.1 Abstract

Measuring dispersal distances is a key challenge limiting progress in seed dispersal research. I used recent advances in modelling approaches to estimate seed dispersal distances generated by frugivorous kereru (New Zealand pigeon, *Hemiphaga novaeseelandiae*). Mechanistic seed dispersal models combine data on frugivore movement patterns and seed retention times. I collected data on kereru daily movement patterns by radio-tracking 24 individual kereru in the Taranaki and Canterbury regions of New Zealand. Kereru were tracked for a total of 43 tracking-days during the peak fruiting season. I followed each individual continuously for up to eight and a half hours, recording kereru residence times and locations visited.

Kereru exhibited sedentary behaviour, with a mean residence time of 32 (± 39) minutes between flights. The longest time recorded at one location was five and a quarter hours. Kereru movements were highly variable, with a mean flight distance of 77 (± 159) m and ranging up to 1, 457 m in a single flight.

I estimated kereru seed dispersal distances by combining the radio-tracking movement data with seed retention times for *Beilschmiedia tawa* (tawa), *Vitex lucens*

(puriri), and *Pseudopanax arboreus* (fivefinger). Kereru dispersed 66–87% of ingested seeds away from the parent tree. Estimated mean seed dispersal distances for tawa, puriri, and fivefinger were 95, 98, and 61 m respectively. The maximum dispersal distance was 1,469 m for all species. Seed dispersal kernels estimated for all three species were right-skewed and leptokurtic in shape, with between 79–88% of seeds dispersed within 100 m of the source and a small number of long-distance dispersal events.

3.2 Introduction

The spatial distribution of seeds is fundamentally important in the ecology and evolution of plants. Seed deposition patterns can influence individual survival prospects (e.g. Howe *et al.* 1985; Wenny 2000), community composition (Christian 2001), gene flow and genetic structure (Gibson & Wheelwright 1995; Hamilton 1999), metapopulation dynamics (Purves & Dushoff 2005), and colonisation rates (Clark et al. 1998b).

Difficulty in quantifying the spatial distribution of seeds has significantly hindered progress in seed dispersal research. Traditional methods such as the use of seed traps or transects tend to underestimate seed dispersal distances by measuring to the nearest adult plant, which is not necessarily the parent (Godoy & Jordano 2001). In addition, studies using these methods are generally unable to detect long-distance dispersal events due to their rarity and issues of scale (Nathan et al. 2003). Recently-developed molecular techniques can overcome these limitations, both quantifying local dispersal and providing an estimate of long-distance dispersal (Godoy & Jordano 2001). However, these techniques require the development of molecular markers and the mapping and genetic identification of every reproductive adult in the population (Godoy & Jordano 2001).

Modelling approaches have also been used to quantify seed deposition patterns. Phenomenological models fit a mathematical function to observed data, describing dispersal patterns but ignoring dispersal processes (Nathan et al. 2003). Mechanistic models combine data on traits of both plants and their dispersal agents to estimate the magnitude and frequency of seed dispersal distances (Nathan & Muller-Landau 2000; Nathan et al. 2003). For vertebrate-dispersed plants, seed deposition patterns result primarily from the movement and behaviour of animal dispersers (Westcott et al. 2005). Mechanistic modelling was first used for vertebrate-dispersed seeds by Murray (1988) and has since been refined by subsequent authors (Sun et al. 1997; Holbrook & Smith 2000; Westcott & Graham 2000; Westcott et al. 2005; Russo et al. 2006). One of the advantages

of mechanistic models is that they can help determine the key factors influencing the dispersal process (Nathan & Muller-Landau 2000; Westcott et al. 2005). Unlike phenomenological models, mechanistic models can predict dispersal distances independently of the observed data (Nathan et al. 2003).

I used a mechanistic modelling approach to estimate seed dispersal distances for an important New Zealand frugivore, the New Zealand pigeon (kereru, *Hemiphaga novaeseelandiae*, Columbidae). Following human arrival in New Zealand, a number of large-bodied birds were driven to extinction (Holdaway et al. 2001). Kereru are virtually the only remaining disperser of large-seeded plants in New Zealand (McEwen 1978; Clout & Hay 1989). I asked the following questions:

1. Does kereru foraging activity vary throughout the day?
2. What is the distribution of kereru residence times?
3. Do kereru residence times differ depending on time of day?
4. What is the distribution of kereru flight distances within a day?
5. Do kereru residence times during foraging differ among fleshy-fruited plant species?
6. What is the seed dispersal kernel generated by kereru?
7. Does the seed dispersal kernel differ among plant species?
8. Does seed dispersal distance increase with increasing seed size among plant species?

3.3 Methods

3.3.1 Study species

The kereru is a large (c. 650 g; Clout et al. 1995b) pigeon that eats only fruits, flowers, and (when fruit is scarce) leaves (McEwen 1978; Clout & Hay 1989). Kereru swallow fruits whole and defecate the seeds intact. Although regurgitation is common for many avian frugivores (Levey 1986), it has been reported only twice for kereru (McEwen 1978; Wotton et al. in press). Kereru consume fruits of at least 70 different plant species (Clout & Hay 1989), across a wide range of fruit sizes. Kereru are capable of flying long distances and tend to migrate seasonally, often following sources of preferred fruit (Clout *et al.* 1986; Clout *et al.* 1991). Although kereru are widespread throughout New Zealand, they

are threatened by habitat loss, predation by introduced mammalian pests, and illegal hunting (McEwen 1978; Clout et al. 1995a; Clout et al. 1995b).

I modelled seed dispersal distances for three fruit species eaten by kereru: tawa (*Beilschmiedia tawa*, Lauraceae), puriri (*Vitex lucens*, Verbenaceae), and fivefinger (*Pseudopanax arboreus*, Araliaceae). Plant names follow Poole and Adams (1990). Tawa is a canopy tree up to 30 m tall, found from northern New Zealand to as far south as Kaikoura (Poole & Adams 1990). Tawa has large fruits measuring 15 x 25 mm (Wotton & Ladley in press), which are important in the diet of kereru (McEwen 1978). Tawa fruits contain a single large seed weighing 2.0 g (mean air-dried weight; DMW unpublished data) and measuring 12 x 24 mm (Wotton & Ladley in press).

Puriri is a canopy tree up to 20 m tall found in northern New Zealand as far south as Taranaki, with large, spherical fruits around 20 mm in diameter (Poole & Adams 1990). The dispersal unit of puriri (for convenience hereafter referred to as a seed) consists of between one to four seeds enclosed in a woody endocarp (Godley 1971), which remains intact after ingestion (Webb & Simpson 2001). Puriri fruits are also an important food item for kereru and seeds weigh 0.67 g (mean air-dried weight, DMW unpublished data).

Fivefinger is a small tree reaching 8 m, found throughout New Zealand. The compressed fruits of fivefinger are 6–8 mm in diameter (Poole & Adams 1990) and contain a single small seed weighing 0.0063 g (mean air-dried weight, DMW unpublished data).

3.3.2 Study sites

This study was replicated at two sites, in the Taranaki and Canterbury regions of New Zealand, from January to April 2006. Study sites in Taranaki were located in New Plymouth (39° 04′ S 174° 05′ E) at Pukekura Park and surrounding urban areas (with both native forest and introduced vegetation), and in small native forest reserves in and near New Plymouth surrounded by an urban or rural matrix. Taranaki sites ranged in altitude from 14–176 m.

Canterbury sites were located on Banks Peninsula at Hinewai Reserve (43° 50′ S 173° 03′ S) and adjacent farmland, and in the nearby settlement of Akaroa (43° 49′ S 172° 58′ E). Hinewai is a 1,050-ha nature reserve dominated by scrub and regenerating native forest, and is surrounded by farmland with small native forest remnants. Akaroa sites were located both in urban Akaroa and in a nearby native forest fragment. Canterbury sites ranged in altitude from sea level to 806 m.

3.3.3 Radio-tracking

I radio-tracked 13 kereru in Taranaki (7 females and 6 males) and 11 individuals in Canterbury (five females, three males, and three of unknown sex). Kereru in Taranaki were fitted with Sirtrack radio-transmitters between August 2004 and September 2005 by the Department of Conservation (R. G. Powlesland, personal communication). Kereru in Canterbury were captured in February 2004 at Hinewai Reserve and transmitters attached by Department of Conservation and Lincoln University (Campbell 2006). I tracked nine of the Canterbury kereru at Hinewai Reserve and on adjacent properties, and two in Akaroa.

I made two trips to each region, with a total of 25 tracking sessions in Taranaki during January and March 2006, and 18 tracking sessions in Canterbury during February and late March to early April 2006. These times coincided with the peak availability of ripe fruit. Each kereru was followed for one to three days in total and not more than twice during each trip. I tracked only those kereru that were not nesting at the time of the study.

I followed kereru continuously using Sirtrack TR4 and R1000 receivers and 160 MHz folding Yagi antennas. I tracked kereru for up to eight and a half hours between the hours of 8 am and 5.30 pm. I recorded each location at which an individual was found throughout the day, using a Garmon Etrex Global Positioning System (GPS) unit where possible. Where a GPS reading was not possible (e.g. due to the terrain or dense forest canopy) I recorded locations using a compass bearing and an estimated distance from a nearby GPS waypoint or from 1:50,000 NZMS260 topographical maps. To limit observer interference with kereru behaviour, I used radio-transmitter signal strength and binoculars to confirm each location from >10 m away where possible. I took GPS location readings after the kereru's departure where observer proximity was likely to cause disturbance. At each location I also recorded (where possible) arrival and departure times, kereru activity, plant species occupied, and the number and species of any fruits consumed.

3.3.4 Statistical analysis

I calculated kereru residence times by subtracting from the arrival time at each location the time of departure from the previous location. Kereru generally took less than a minute to fly between locations. For locations at the start and end of tracking sessions, I only knew the kereru arrival and departure time for those sessions that started or ended with a flight. For remaining start and end locations I was unable to determine exact residence times. However, first and/or last residence times sometimes contributed a significant proportion to the duration of a tracking session. For example, one kereru stayed at the same location

for the entire period of a five-hour tracking session. To include this important data, I estimated residences times at the start and end locations using either the start or end time of the tracking session as the arrival or departure time. Because of the uncertainty associated with residence time estimates, I only included estimated times longer than one hour, as the error in estimation should decrease with increasing residence time and longer residence times made up a greater proportion of a tracking session. Prior to analysis, I removed all residence times where observer proximity may have startled the kereru into flight. Kereru residence time data were log-transformed to improve normality. I then used ANOVA, with bird as a random effect, to test for differences in mean kereru residence time between Taranaki and Canterbury.

For each kereru location the distance between this location and every other location in the same tracking session (i.e. for the same bird on the same day) was calculated using ArcInfo GIS software. Flight distance data were log-transformed to improve normality before testing for differences in mean flight distance between regions using ANOVA, with bird as a random effect. I tested for differences among plant species in kereru residence time while foraging on fruit using ANOVA. All data were analysed using R version 2.1.1 (R Development Core Team 2005).

3.3.5 Model structure

A seed shadow describes deposition patterns relative to parent plants and other conspecifics and is a function of both the distance and the direction of seed dispersal (Janzen 1970; Godoy & Jordano 2001). A seed dispersal kernel (also referred to as a dispersal curve) is a one-dimensional probability distribution of dispersal distances (Skarpaas et al. 2005). I developed a mechanistic seed dispersal model to estimate kereru dispersal kernels for tawa, puriri, and fivefinger. The model was written in the S language using R version 2.1.1 (Appendix I; R Development Core Team 2005). Seed retention times were simulated by randomly sampling 100 seed retention times from a normal distribution, using the mean and standard deviation from empirical data for each plant species (tawa = 180.8 ± 100.3, puriri = 108.6 ± 57.9, and fivefinger = 37.4 ± 9.9 minutes; Wotton et al., in press).

The model simulated ingestion of these 100 seeds (with retention times generated as above) at each minute of each tracking session. Using the location of the bird at the time of ingestion, and the retention time for that seed, the model determined the location of the kereru at the time of defecation and the distance from the ingestion point for each seed.

The model repeated the procedure for each of 39 tracking sessions. Although I recorded 43 tracking sessions, four tracking sessions were excluded, three due to missing data, and one because it was shorter than the maximum seed retention time.

The model was unable to calculate dispersal distances where a seed retention time ran past the end of the tracking session. One option was to stop the simulation when the time remaining in the tracking session was less than the longest seed retention time. However, this would have excluded a large number of dispersal distances, especially from times later in the day. I therefore decided to allow all possible dispersal distances to be calculated. This means that dispersal distances were biased towards shorter seed retention times.

3.4 Results

3.4.1 Kereru behaviour

I observed kereru feeding on fruits of 19 plant species while radio-tracking, and foraging occurred throughout the day (Figure 3.1). Kereru in Canterbury also fed on leaves of kowhai (*Sophora microphylla*), ribbonwood (*Plagianthus regius*), and mahoe (*Melicytus ramiflorus*). While foraging for fruits, kereru spent more than half of the time feeding on puriri, tawa and cabbage tree (*Cordyline australis*), which contributed 21.6%, 20.6%, and 11.9% to fruit foraging time respectively. The remaining time was spent feeding on fruits of tree fuchsia (*Fuchsia excorticata*. 8.7%), kawakawa (*Macropiper excelsum*, 7.8%), ngaio (*Myoporum laetum*, 7.7%), mahoe (6.0%), kahikatea (*Dacrycarpus dacrydioides*, 5.2%), miro (*Prumnopitys ferruginea*, 2.3%), cherry laurel (*Prunus caroliniana*, 2.0%), rohutu (*Lophomyrtus obcordata*, 1.4%), horopito (*Pseudowintera colorata*, 1.2%), nikau (*Rhopalostylis sapida*, 0.9%), fivefinger (*Pseudopanax arboreus*, 0.7%), kaikomako (*Pennantia corymbosa*, 0.7%), lancewood (*Pseudopanax crassifolius*, 0.6%), kohekohe (*Dysoxylum spectabile*, 0.3%), poroporo (*Solanum sp.*, 0.3%), and titoki (*Alectryon excelsus*, 0.2%). I observed kereru feeding on fruits of only one non-native plant species (cherry laurel), even though other introduced species that kereru have been reported to feed on had ripe fruits at the study sites (e.g. holly, *Ilex aquifolium*; McEwen 1978).

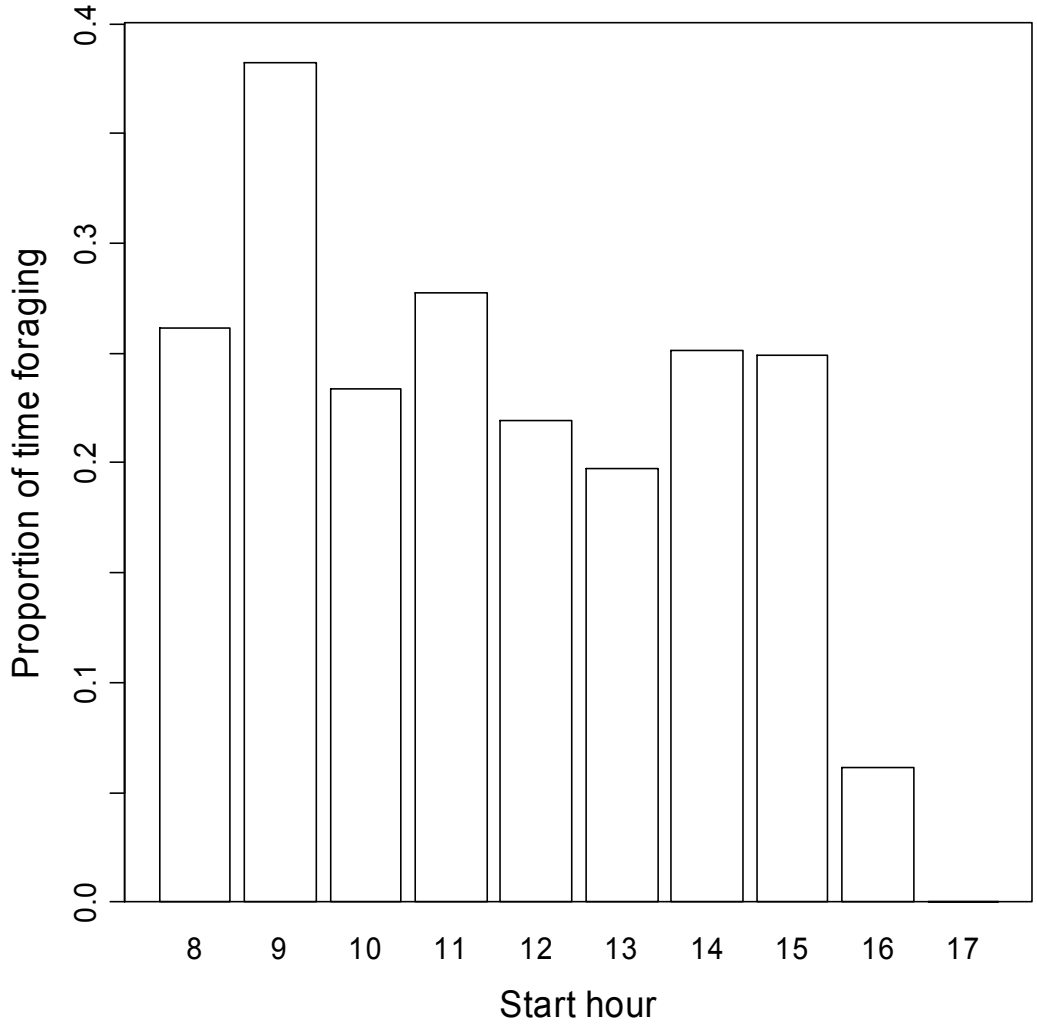


Figure 3.1 Distribution of foraging effort by kereru throughout the day. Time of day was the hour during which the foraging bout commenced.

The mean overall kereru residence time was 32 (± 39 SD) minutes with a median of 19 minutes and a maximum of 315 minutes (Figure 3.2; all means reported in the text are untransformed). Kereru in Taranaki were significantly more sedentary than those in Canterbury, with mean residence times of 37 and 27 minutes respectively (d.f. = 22 and 502, F = 16.796, P < 0.001). Kereru residence times did not differ depending on time of day (Figure 3.3), which did not appear to be important and so was ignored subsequently.

I recorded 528 individual flight distances while radio-tracking kereru. Kereru movements were generally quite localised during the course of the day (Figure 3.4). The mean flight distance was 77 (± 159) m with a maximum observed flight distance of 1,457 m (Figure 3.5). Flight distances were highly right skewed and leptokurtic in shape, with a median flight distance of 32 m. There was no significant difference in mean flight distance between the two regions (d.f. = 22 and 504, F = 0.177, P = 0.678).

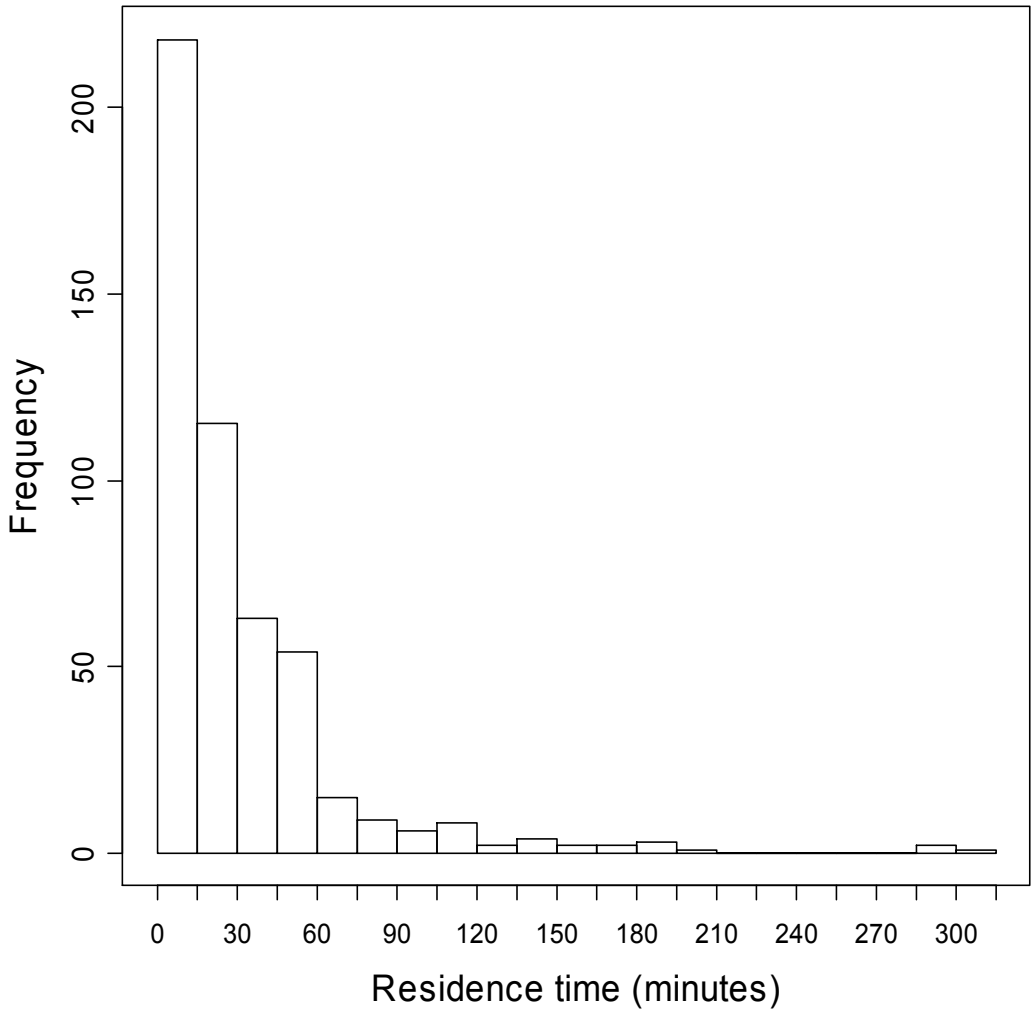


Figure 3.2 Frequency distribution of observed kereru residence times.

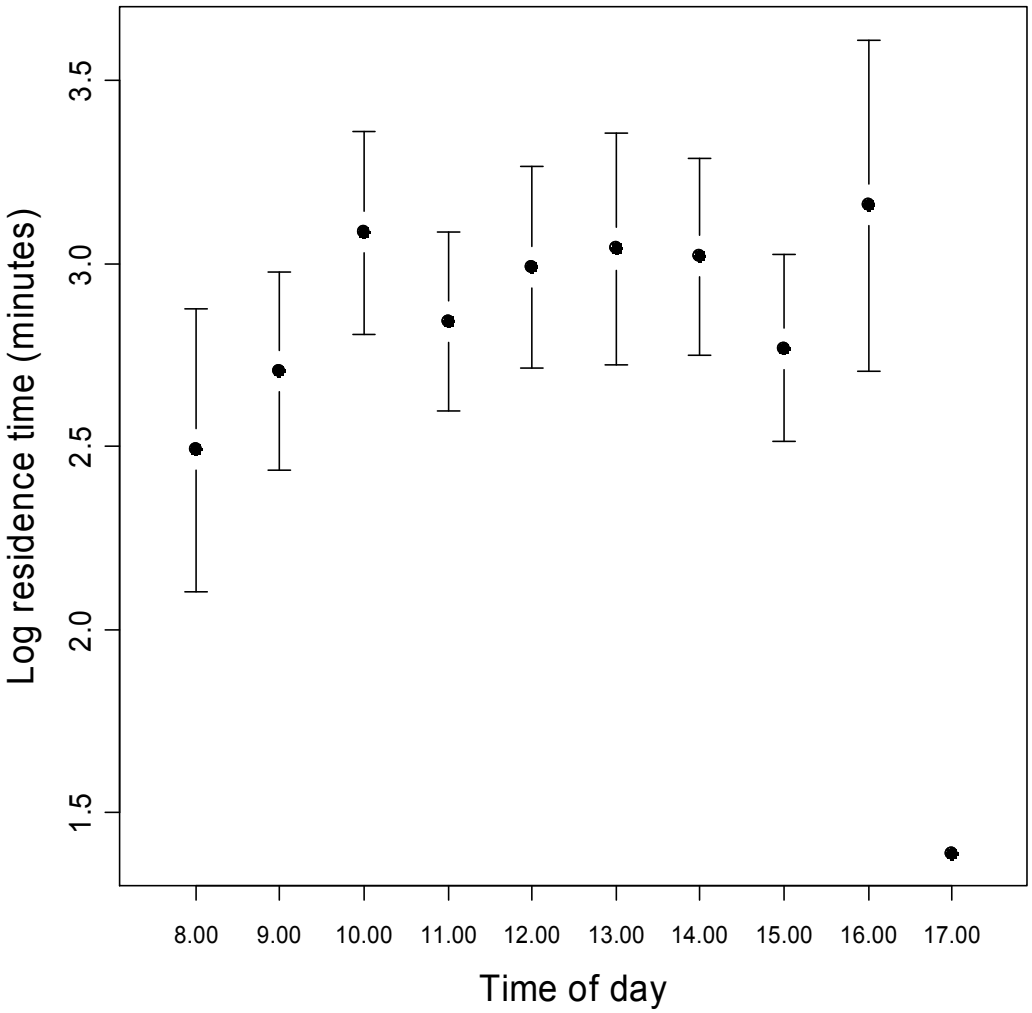


Figure 3.3 Kereru log mean residence time as a function of time of day (taken as the midpoint between arrival and departure times). Error bars are 95% confidence intervals.

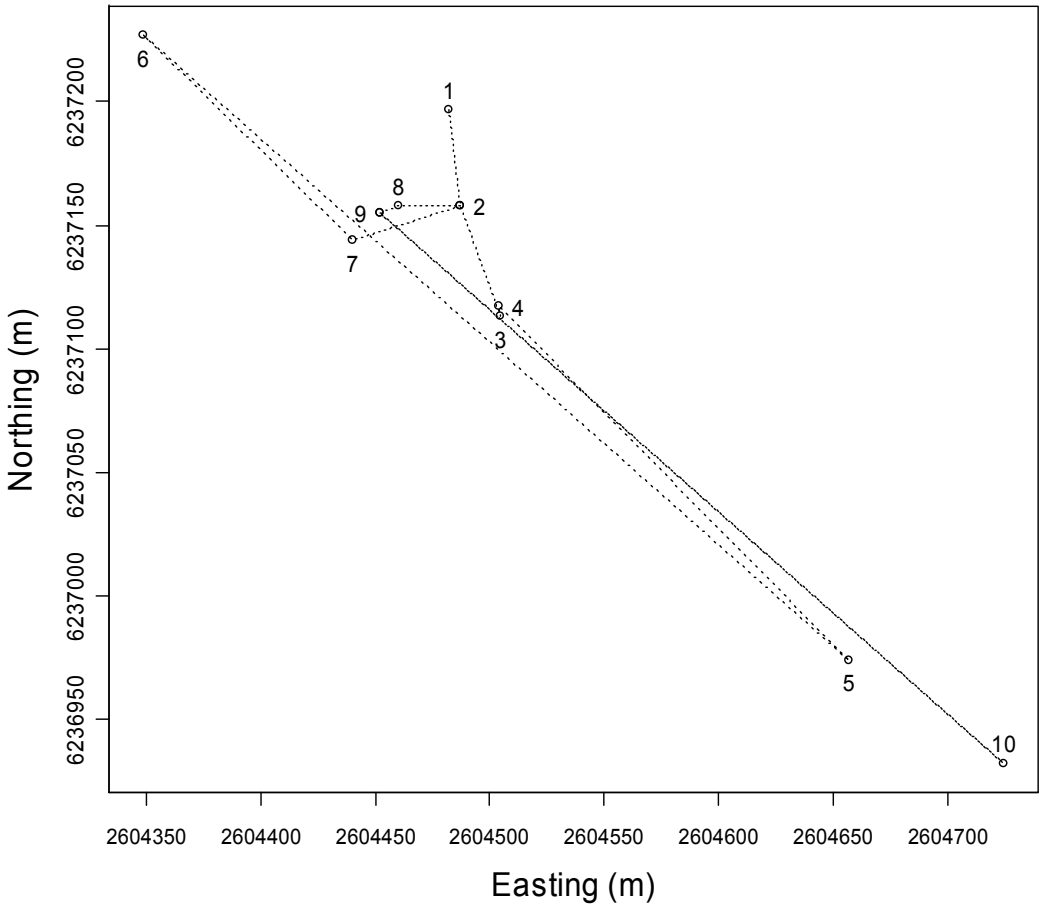


Figure 3.4 Example of a kereru's movement pattern during one day. I tracked this individual continuously for 441 minutes on 5 March 2006, in Taranaki.

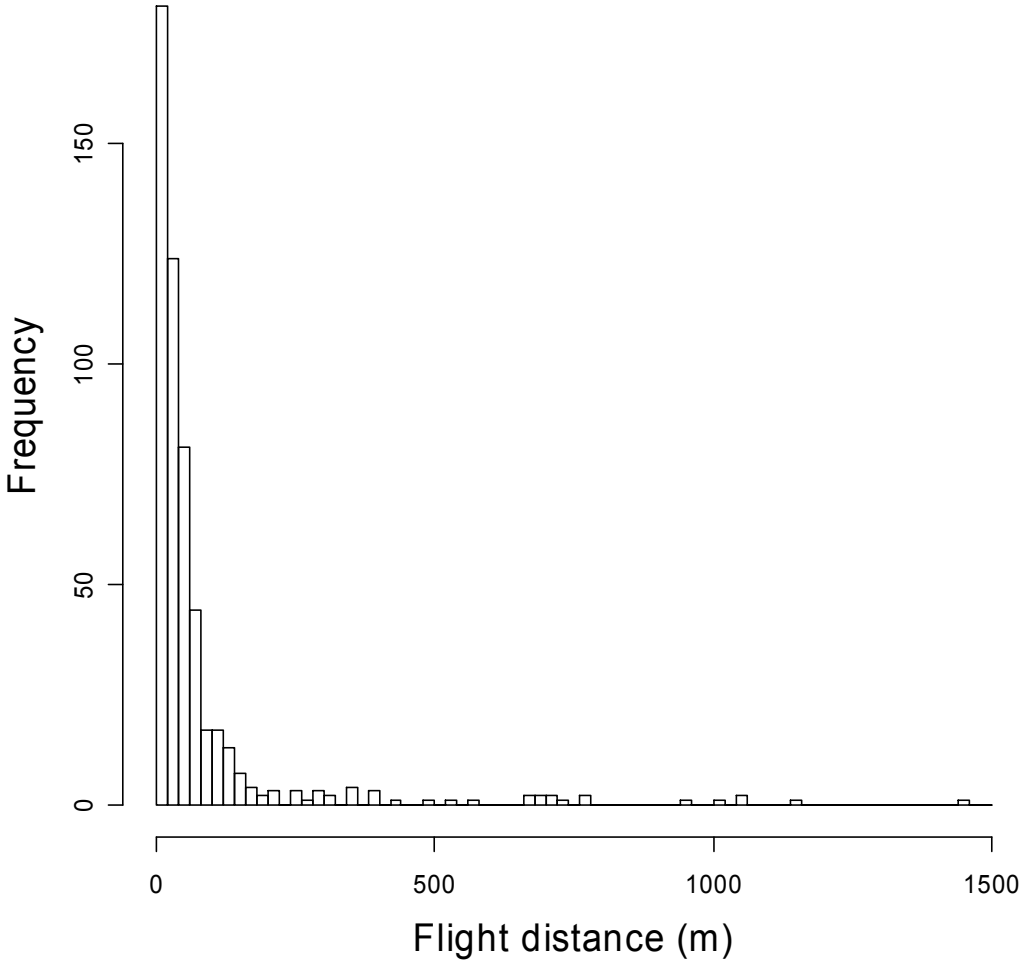


Figure 3.5 Frequency distribution of observed kereru flight distances.

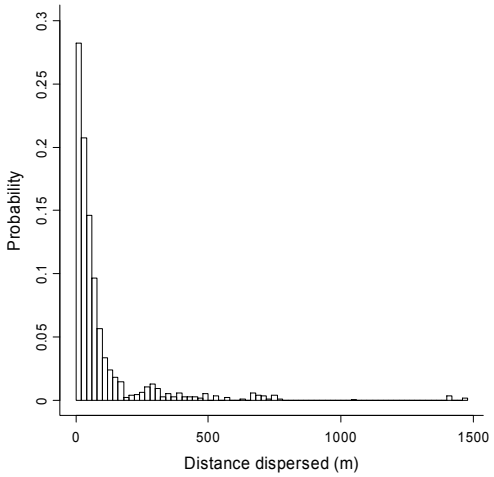
3.4.2 Dispersal distances

The model estimated that kereru dispersed 66–87% of ingested seeds away from the parent tree. Most seeds were deposited within 100 m of the source with less than 1% of seeds dispersed greater than 1 km (Table 3.1). The maximum dispersal distance estimated by the model for all species (1,469 m) was constrained by the maximum distance between two points visited by an individual kereru during radio-tracking. Fivefinger dispersal distances were shorted than puriri and tawa, with a greater proportion of seeds dispersed beneath the parent (Figure 3.6, Table 3.1).

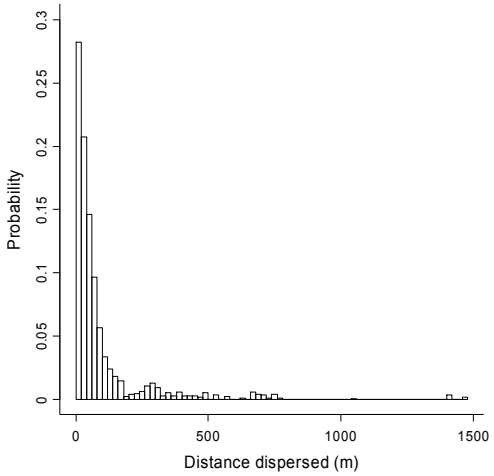
Table 3.1 Kereru seed dispersal distances (m) estimated using a mechanistic model based on empirical data for kereru movements and seed retention times. N = number of seed dispersal "events" simulated by the model, see text for details.

			Seeds dispersed (%)			
Species	Mean (± 1 sd)	Median	0 m	>100 m	>1,000 m	N
Tawa	95 (± 171)	42	12.7	21.0	0.68	754,351
Puriri	98 (± 186)	41	13.4	20.5	0.96	999,061
Fivefinger	61 (± 140)	22	34.3	12.4	0.39	1,299,670

(a)



(b)



(c)

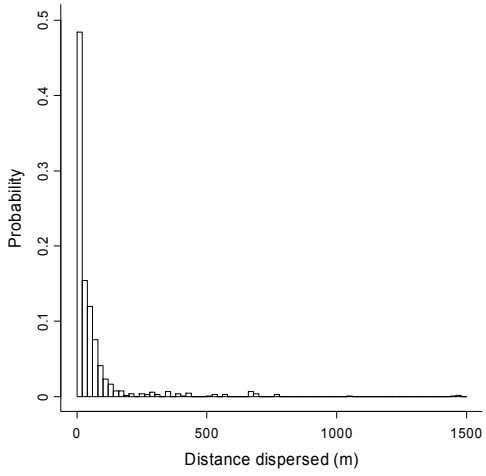


Figure 3.6 Estimated kereru seed dispersal kernels for (a) tawa, *Beilschmiedia tawa*; (b) puriri, *Vitex lucens*; and (c) fivefinger, *Pseudopanax arboreus*. Dispersal kernels were generated using a mechanistic model that incorporated empirical data for individual kereru movements and seed retention times. Note differences in the y-axis scales.

Residence time while feeding on fruit differed significantly among plant species (d.f. = 4, F = 2.74, P = 0.0361; Figure 3.7). Kereru residence times were shortest while feeding on cabbage tree (mean ± 1 s.d. = 15 ± 8.29 minutes). Kawakawa, ngaio, and puriri had similar residence times (25 ± 26.96, 24 ± 32.47, and 29 ± 18.11 minutes respectively), while I recorded the longest residence times when kereru were foraging on tawa (40 ± 21.91 minutes).

Table 3.2 Kereru residence time (minutes) in different plant species while foraging for fruit. Only those species with ten or more foraging observations are shown (N = number of foraging observations). There was a significant difference in mean residence time among fruit species (P = 0.0361).

Fruit species	Scientific name	Mean	SD	Min.	Max.	N
Cabbage tree	*Cordyline australis*	15	8.29	1	38	19
Kawakawa	*Macropiper excelsum*	25	26.96	3	91	10
Ngaio	*Myoporum laetum*	24	32.47	6	118	11
Puriri	*Vitex lucens*	29	18.11	4	59	19
Tawa	*Beilschmiedia tawa*	40	21.91	6	75	14

3.5 Discussion

3.5.1 Kereru behaviour

Despite their ability to fly long distances, kereru were relatively sedentary on a daily basis, often resting for long periods between flights. Kereru residence times (mean 15–40 minutes and up to five and a quarter hours) are generally much longer than reported for other avian frugivores (Pratt & Stiles 1983; Murray 1988; Wheelwright 1991; Sun et al. 1997). Mean residence times for three bird species in Costa Rican cloud forest ranged from 7–12 minutes (Murray 1988). Wheelwright (1991) reported median residence times in fruiting trees of frugivorous birds in Costa Rica ranging from 1–9 minutes. Toucanets occasionally stayed up to four hours in a fruiting tree, and quetzals up to one hour, but the maximum residence time for other birds was 40 minutes (Wheelwright 1991). In a study of ten frugivorous bird species, mean residence times in fruiting trees ranged from 4.5–31.1 minutes (Pratt & Stiles 1983).

Long residence times in kereru may result in part from slow fruit digestion rates (Wotton et al. in press). This is supported by evidence for longer avian residence times after feeding on lauraceous species with large fruits and longer processing times (Wheelwright 1991). Unlike many frugivores (Levey 1987), kereru generally do not regurgitate seeds (McEwen 1978), and can take up to five and a half hours to void large seeds such as tawa (Wotton et al. in press). Because kereru are gut-limited (Wotton et al. in press), long residence times probably minimise energy expenditure while waiting for space to be created in the gut (Wheelwright 1991), and also increase the chance of eliminating the heavy seed "ballast" before flight (Levey & Grajal 1991).

Long residence times may also decrease predation risk, because kereru usually rest among or under the canopy, hidden from avian predators (Bell 1996). Prior to the human introduction of mammalian predators, kereru had only avian predators, including the New Zealand falcon (*Falco novaeseelandiae*) and the giant New Zealand harrier hawk (*Circus eylesi*), which is now extinct (R. N. Holdaway, personal communication). Howe (1979) predicted that foraging behaviour of frugivorous birds will be influenced by predation risk. Some studies support this prediction, showing that larger birds visit fruiting plants for longer than small passerines, which have a higher predation risk and usually remain only long enough to feed (Pratt & Stiles 1983; Green 1993). Kereru usually leave nikau and

cabbage trees shortly after feeding, and these plants generally lack concealed perches (Bell 1996).

Long seed retention times increase the potential seed dispersal range of kereru. Seed size probably affects dispersal distances too, as kereru seed retention times are strongly positively correlated with seed size (Wotton et al. in press). Rapid digestion rates in fivefinger reduced both the proportion of seeds dispersed away from the parent and the average seed dispersal distance (Table 3.1). Nevertheless, the maximum dispersal distance (1,469 m) was the same for all species, as estimated dispersal distances were constrained by the maximum distance that I recorded between two locations within a tracking session. Occasional longer dispersal distances, especially for species such as tawa that have long retention times, are probable.

Kereru are capable of flying considerable distances, migrating kilometres or tens of kilometres on a seasonal basis, often tracking fruit availability (Clout *et al.* 1986; Clout *et al.* 1991). Harper (2003) observed kereru crossing Foveaux Strait between South and Stewart Islands, an estimated flight of 32 km with at least 25 km of this over sea. My study was too short in duration to detect such long-distance movements, which appear to be infrequent. In addition, I radio-tracked kereru on foot. In Taranaki, some kereru that were radio-tracked in New Plymouth during the first trip were unable to be located during the second visit. Department of Conservation researchers subsequently detected them using aerial surveys in Taranaki National Park, at least 15 km from New Plymouth. Kereru probably migrated to feed on miro fruits, which are common in lowland areas of the National Park and were ripening at the time (Sarah Kivi, personal communication, April 2006). Kereru usually defecate while perching and only occasionally while in flight (McEwen 1978). Therefore, kereru would tend to void seeds either prior to a long flight or after reaching a new destination, although the chance of defecation in flight might be expected to increase with the duration of the flight.

3.5.2 Dispersal distances

The estimates of kereru dispersal kernels were all relatively similar in shape, regardless of tree species. Kereru deposited many seeds close to the source, with a rapid decline in seed density away from the "parent" and less than 1% of seeds dispersed greater than 1,000 m. The shape of kereru dispersal kernels suggests a leptokurtic distribution. Dispersal kernels estimated for hornbills resembled a Poisson distribution (Holbrook & Smith 2000), while those for spider monkeys best fit a mixture distribution (Russo et al. 2006).

My estimates of kereru dispersal distances are comparable to dispersal distances by spider monkeys (Russo et al. 2006) and cassowarys (Westcott et al. 2005). Holbrook and Smith (2000) used a mechanistic model to estimate maximum seed dispersal distances by hornbills of nearly 7 km. Estimates for turaco mean seed dispersal distances were greater than for kereru, but maximum dispersal distance estimates were not reported (Sun et al. 1997). Westcott and Graham (2000) estimated that a small flycatcher dispersed seeds up to 100 m, with mean distances of 21–46 m. Kereru dispersed 66–87% of ingested seeds away from the parent tree. Other studies generally have not reported the proportion of ingested seeds deposited by dispersers beneath the parent plant. However, dispersers of *Prunus mahaleb* deposited 18–24% of seeds beneath the canopies of adult conspecifics (Jordano et al. 2007). For small to medium-sized birds, 17–19% of seeds under *P. mahaleb* canopies came from another population, while for mammals nearly 80% of seeds under conspecifics were immigrants (Jordano et al. 2007).

The foraging behaviour of kereru differs among plant species (Bell 1996, Figure 3.7) and is highly likely to influence seed dispersal kernels. The length of time kereru stay in a fruiting tree is probably influenced to a large extent by tree architecture. Species such as cabbage tree and nikau generally do not provide easy perching sites for kereru. On more than one occasion I observed kereru losing their balance and falling while feeding on cabbage tree fruits.

Kereru may be more effective dispersers for those species where departure takes place soon after feeding. For example, when feeding on cabbage tree fruits, kereru usually remained in the same tree for around 15 minutes. This contrasts to those species which are favoured as resting sites, such as tawa where the mean residence time when foraging was 40 minutes. Bell (1996) showed that kereru were most likely to depart soon after feeding in nikau and kahikatea, and least likely in puriri. To improve the accuracy of the estimated dispersal kernel, the model could simulate fruit ingestion only at times corresponding to when kereru were actually observed in that plant species. For example, dispersal distances may be greater than estimated in a small-seeded species such as fivefinger if residence times are shorter than average. I was unable to test whether the variation in residence time among fruiting species influences the dispersal kernel, due to insufficient replication of visits to fruiting species and/or lack of seed retention time data. These differences in kereru behaviour are most likely to affect dispersal of small-seeded species, for which alternative seed dispersers are available. The current model provides a good approximation for the large-seeded species tawa and puriri, for which kereru are virtually the sole dispersers.

3.5.3 Conservation implications

Kereru densities have declined significantly since the arrival of humans (Clout & Hay 1989). Changes in kereru abundance could affect both the probability of dispersal and seed dispersal distances. McConkey and Drake (2006) demonstrated that flying foxes in Tonga only provide effective dispersal at high bat densities, when aggressive interactions occur. At low bat densities flying foxes dispersed less than 1% of seeds away from parents. Although the consequences are unlikely to be as extreme in this study system, kereru behaviour appears to change when bird densities are high. Kereru often defend fruiting trees of favoured species such as miro (*Prumnopitys ferruginea*) and kahikatea, which may cause individuals to move elsewhere when denied access to fruit locally (Clout et al. 1991). This is likely to increase both total dispersal, with shorter residence times in fruiting trees, and the probability of long-distance dispersal, with more frequent movements between forest patches.

Landscape structure may also influence seed dispersal distances. Much of New Zealand's forest habitat was destroyed by both Maori and European settlers, creating a mosaic of forest remnants interspersed with agricultural and urban areas. I conducted this study in fragmented habitats, in which kereru movement patterns may differ compared to those occurring in continuous forest. However, food supply may have a greater influence on movement patterns as kereru readily fly between forest patches. The consequences of forest fragmentation for genetic structure and gene flow in large-seeded species in New Zealand are unknown, but movement of kereru between forest patches may be essential in maintaining fragmented metapopulations of large-seeded trees.

Chapter 4. Effects of kereru gut passage on *Beilschmiedia tarairi* seed germination

Kereru-defecated taraire (*Beilschmiedia tarairi*) seed.

4.1 Abstract

I tested the effects of gut passage (scarification) and pulp removal (deinhibition) on seed germination of the fleshy-fruited tree *Beilschmiedia tarairi*. I conducted a germination experiment under natural field conditions using hand-cleaned seeds, seeds freshly defecated by wild kereru (New Zealand pigeon, *Hemiphaga novaeseelandiae*), and whole fruits. Seed treatment had a significant effect on germination percentage, which was higher for kereru-defecated seeds (mean 96%) than hand-cleaned seeds (83%) and seeds in whole fruits (75%). The scarification effect was greater than the deinhibition effect, which was not statistically significant. Kereru-defecated seeds also germinated faster than hand-cleaned seeds and seeds in whole fruits.

4.1.1 Introduction

Animal seed dispersers can influence the fitness of plants by affecting the quantity and quality of dispersal (Schupp 1993). The treatment of seeds in dispersers' guts is one aspect of seed dispersal quality (Schupp 1993). Frugivores can affect germination success by

three mechanisms: (1) the scarification effect — scarification of the seed coat, which may enhance germination by improving the absorption of water and gases by the seed, or may reduce germination if physical or chemical treatment of the seed is too vigorous; (2) the deinhibition effect — removal of germination inhibitors contained in the fruit pulp; and (3) the fertilisation effect — nourishment of the seed and seedling from faecal material defecated with the seed (Traveset & Verdú 2002; Robertson et al. 2006).

Ingestion by dispersers can enhance germination success, although very few or perhaps no species have seeds that absolutely require gut passage in order to germinate (Rick & Bowman 1961; Traveset 1998). However, few studies have compared germination of whole fruits and ingested seeds (the two naturally occurring seed fates), and most studies are carried out under artificial conditions (Kelly et al. 2004; Samuels & Levey 2005; Robertson et al. 2006). Therefore, we know little about the likely consequences in the field of dispersal failure (Robertson et al. 2006).

Following the arrival of humans to New Zealand, a number of large-bodied birds were driven to extinction (Holdaway et al. 2001). Other previously widespread bird species were restricted to a tiny fraction of their former ranges, and the density of most remaining species was drastically reduced (Clout & Hay 1989). One of the consequences of this devastation of New Zealand's avian fauna is that a number of large-seeded species now rely on a single frugivore, the New Zealand pigeon (kereru, *Hemiphaga novaeseelandiae*), for their dispersal (Clout & Hay 1989). Although kereru are widespread throughout New Zealand and relatively common, they are threatened by habitat loss, predation by introduced mammalian pests, and illegal hunting (McEwen 1978; Clout et al. 1995a; Clout et al. 1995b). Given the apparent vulnerability of these large-seeded species to dispersal failure, I investigated whether kereru gut passage and fruit pulp removal are beneficial to germination of the large-seeded tree taraire (*Beilschmiedia tarairi*), for which the kereru is the only extant bird large enough to swallow its fruits. I tested the following hypotheses:

1) Germination success is higher for hand-cleaned seeds than whole fruits (a deinhibition effect occurs)
2) Germination success is higher for kereru-defecated seeds than hand-cleaned seeds (a scarification effect occurs)

Given that kereru are primarily frugivorous (McEwen 1978), and guided by the most common results in the literature (Traveset & Verdú 2002; Samuels & Levey 2005; Robertson et al. 2006), I predicted that the treatment of seeds in the gut was likely to be gentle, primarily enhancing germination success by removing pulp from the seed. I did not

test for a fertilisation effect, because faecal material is virtually absent when kereru defecate large seeds (DMW personal observation).

4.2 Methods

4.2.1 Study species and sites

Kereru are large fruit pigeons endemic to New Zealand weighing around 650 g (Clout et al. 1995b). They are primarily frugivorous, but also eat flowers and leaves when fruits are scarce (McEwen 1978). Kereru are an important seed disperser, consuming fruits of more than 70 plant species. Kereru generally swallow fruits whole and defecate the seeds intact (McEwen 1978; Wotton et al. in press).

Taraire is a large-seeded tree with single-seeded fruits measuring 19 x 32 mm (mean diameter x length) and seeds measuring 16 x 29 mm (Wotton & Ladley in press). Taraire occurs in coastal and lowland forest in northern New Zealand and fruits are important in the diet of kereru (McEwen 1978). I conducted research at Mt Tiger Bush, Whangarei (35° 43′ S, 174° 23′ E) from September to December 2005. The study site was located in a 7-ha privately owned block that forms part of the 267-ha Mt Tiger Bush. The site is mainly towai (*Paratrophis banksii*)-dominant secondary lowland forest, ranging in altitude from 140–270 m.

4.2.2 Experimental design

I conducted the germination experiment in the field rather than glasshouses, as recent evidence indicates that laboratory and greenhouse trials are less relevant and less likely to detect actual differences than field trials (Traveset & Verdú 2002; Robertson et al. 2006). I used a randomised, nested block experimental design with three levels of seed treatment: hand-cleaned seeds, kereru-defecated seeds, and whole fruits. I selected five adult taraire trees located throughout the study site. At each tree I established a pair of plots, one plot beneath the adult taraire tree and another 20 m away. I randomly assigned the three seed treatments to each experimental unit within a plot (ten plots in total).

I collected ripe fallen taraire fruits and kereru-defecated seeds from privately owned forest in Whangarei nearby to the study site. I used only whole fruits that were free from insect attack and freshly defecated seeds in the experiment. The hand-cleaned and whole fruit treatments were also used as part of a long-term seed fate experiment and had 20 seeds or fruits per experimental unit (see Chapter 5 for details). I was able to collect

only 70 freshly defecated taraire seeds; therefore this treatment had seven seeds for each experimental unit.

To prevent seeds rolling away I used 7 cm wide strips of lexan polycarbonate (1 mm thick) with the ends stapled together to construct 20 cm diameter tubes. Tubes were inserted into the soil approximately 1 m apart with around 5 cm of the tube remaining above ground. I placed seeds inside tubes and covered them with mammal-proof cages constructed of 5.8 mm aperture stainless steel weldmesh. Cages and tubes were secured to the ground with wire pegs. I sowed seeds in September 2005 and checked the experiment monthly, recording germination percentage until all seeds had either germinated or rotted. At each visit, I placed any litter found on top of the cage inside the tube to minimise the effect of leaf litter interception by cages.

4.2.3 Statistical analysis

I analysed the germination data using a binomial generalised linear mixed model with a logit link function. I fitted the model using the Laplacian approximation to maximum likelihood, with seed treatment as a fixed effect and plots nested within trees as random effects. Distance from parent was not included as a variable in the model, as it had no effect on taraire germination success in a concurrent seed fate experiment (Chapter 5). I carried out the analysis using the lme4 package in R version 2.4.1 (R Development Core Team 2006).

4.3 Results

Taraire seeds began germinating within one month of sowing, and all seeds had either germinated or rotted within three months. Seed treatment had a significant effect on germination success (d.f. = 2, SS = 12.2098, MS = 6.1049, deviance = 24.98; Table 4.1). Seeds defecated by kereru had significantly higher germination success (mean ± 1 s.d. = 95.7 ± 9.6 %) than hand-cleaned seeds (82.5 ± 8.6%) and seeds in whole fruits (75 ± 6.7%; Table 4.1). In other words, kereru gut passage had a significant effect on germination success due to seed scarification. The effect of pulp removal (the deinhibition effect, i.e. hand-cleaned versus whole fruits) was not statistically significant (Table 4.1). Kereru-defecated seeds also germinated faster than both hand-cleaned seeds and seeds in whole fruits (Figure 4.1).

Table 4.1 Effects of scarification (hand-cleaned vs. kereru-defecated seeds) and deinhibition (hand-cleaned seeds vs. whole fruits) on germination success of taraire (*Beilschmiedia tarairi*) seeds. I analysed data using a binomial generalised linear mixed model with a logit link function.

	estimate	s.e.	z-value	P
intercept (hand-cleaned)	1.55	0.19	8.33	<0.001
defecated	2.00	0.75	2.67	0.008
whole fruits	– 0.45	0.25	–1.82	0.069

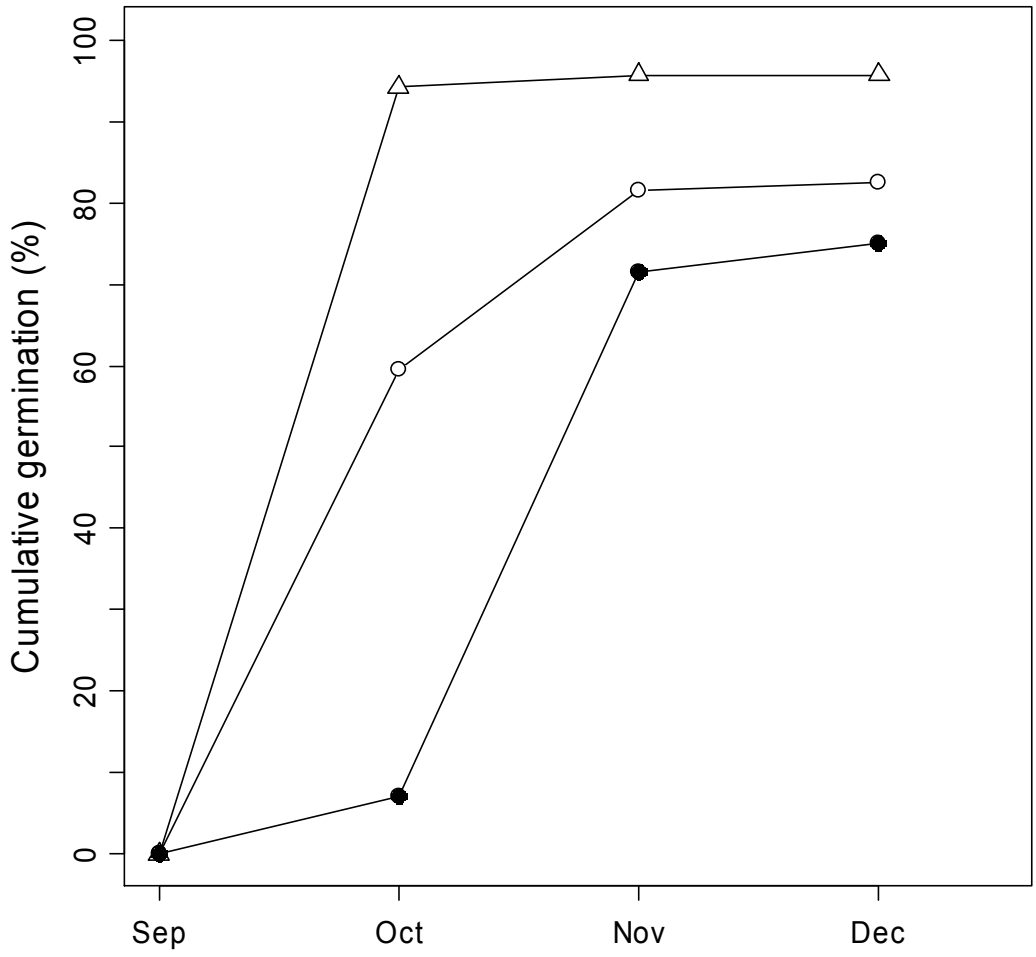


Figure 4.1 Effect of seed treatment on mean germination speed in taraire (*Beilschmiedia tarairi*). Filled circles = whole fruits, open circles = hand-cleaned seeds, open triangles = kereru-defecated seeds.

4.4 Discussion

Large-seeded plant species are more vulnerable to dispersal failure, as fewer frugivores are large enough to swallow fruits and disperse seeds (Wheelwright 1985; Clout & Hay 1989; Kitamura et al. 2002). Of these large-seeded species, those that require removal of the fruit pulp or seed scarification in order to germinate are most likely to be dependent on seed dispersal mutualisms (Kelly et al. 2004). There have been many tests of the scarification effect, which generally enhances germination in fleshy-fruited species (Traveset & Verdú 2002). However, few studies have included whole fruits as a treatment, which allows the deinhibition effect (and consequently the total effect of gut passage on germination success) to be tested (Samuels & Levey 2005; Robertson et al. 2006). Previous trials with miro (*Prumnopitys ferruginea*) using whole fruits and kereru-defecated seeds showed no difference in germination success between the two treatments, but this plant has especially recalcitrant seeds that can take more than 4 years to germinate (Clout & Tilley 1992).

In addition, most experiments have been conducted under artificial conditions (Traveset & Verdú 2002). Under natural field conditions, seeds are exposed to the elements and other biota that can enhance leaching of pulp inhibitors and break down of the fruit pulp (Kelly et al. 2004; Robertson et al. 2006). Some microbes that occur under natural conditions enhance germination success (Morpeth & Hall 2000), while others kill the seed embryo (Titus et al. 1990). Burrows (1996) reported zero germination of karaka seeds within whole fruits, indicating this species could be dependent on seed dispersal in order to germinate. However, seeds were germinated in petri dishes in the laboratory (Burrows 1996); subsequent trials in the field show that karaka seeds do germinate in whole fruits when under natural conditions (Robertson et al. 2006, Chapter 4). Taraire seeds did not require pulp removal in order to germinate, although kereru gut passage enhanced germination success. Although kereru-ingested seeds germinated faster than hand-cleaned seeds and whole fruits, the difference is not likely to have a significant effect on long-term survival.

Some of the potential drawbacks of using naturally-defecated seeds include unknown seed age, limited availability, and non-random selection of fruits by frugivores (Robertson et al. 2006). I used only freshly defecated seeds and fruits that had no sign of decay or insect attack in the experiment. However, because freshly defecated seeds were relatively scarce, seed density differed among the treatments. Results from this experiment need to be interpreted in light of findings from the seed fate experiment (Chapter 5), where

whole fruits had greater germination success at high density (75%, 20 seeds) than at low density (65%, 4 seeds), while the reverse was true for hand-cleaned seeds (82.5% at high density and 97.5% at low density). Thus, density may be confounded with seed treatment in this experiment, due to fewer defecated seeds than hand-cleaned seeds or whole fruits. The effect of seed density on germination success of defecated seeds is unknown, but may be similar to hand-cleaned fruits.

In this experiment, the scarification effect was greater than the deinhibition effect, which was not statistically significant. Nevertheless, kereru gut passage appears to have enhanced germination success compared to whole fruits. Although the mechanism (deinhibition and/or scarification) was unclear in this experiment, the seed fate experiment demonstrated that fruit pulp removal increased germination success. In experiments conducted under artificial conditions, fruit pulp removal consistently increased taraire germination success, while seed scarification (after kereru gut passage) increased germination success in one study but not in the other (Myers 1984; Bell 1996). Ideally this experiment should be repeated in the field using equal seed densities in all treatments to confirm whether kereru gut passage enhances taraire germination success through seed scarification.

Kereru gut passage and fruit pulp removal both enhanced germination speed (Figure 4.1). Although the increase was relatively small (1–2 months) it may be important for enabling taraire seedlings to establish prior to dry summer conditions. However, early germination is not always beneficial (Robertson et al. 2006). In some plant species, delayed germination in whole fruits may be a strategy for dispersing seeds in both space and time (Robertson et al. 2006).

Defecated seeds used in this experiment may have been a non-random sample, if kereru selected fruits non-randomly from those available (Robertson et al. 2006). Fruit selection may differ depending on factors such as size (Wotton & Ladley in press), degree of ripeness, presence of pathogens, or insect infestation. Where defecated seeds have a greater germination success than hand-cleaned seeds, dispersal will still be beneficial to plants whether the increase is due to frugivore selection of higher viability seeds or to scarification. Because I was not able to collect taraire fruits directly from the canopy, whole fruit and hand-cleaned seed treatments were also non-random samples. Interestingly, Myers (1984) tested germination from intact taraire fruits collected from the ground and from the canopy in two consecutive years and in both years found lower germination for those collected from the ground; however, she thought this was related to insect predation

and fallen fruits drying out, which I tried to minimise by only collecting apparently uninfested, freshly-fallen fruits. Randomly selected fruits could be fed to captive kereru to control for any effects of fruit selection by kereru.

Nevertheless, this study suggests that dispersal failure will have significant detrimental effects on the germination of taraire seeds. Unusually, in this case the major benefit of handling by frugivores seems to be from the scarification effect rather than the deinhibition effect (c.f. Robertson et al. 2006). However, the overall magnitude of the effect (a one-fifth reduction in germination, from 96% to 75% of seeds) is much smaller than that postulated for other large-seeded species on the basis of laboratory germination trials (Kelly et al. 2004).

Chapter 5. Consequences of dispersal failure for large-seeded trees

Wenderholm Regional Park, north of Auckland.

5.1 Abstract

When animal seed dispersers are lost and their services are not replaced, seeds remain undispersed and fall beneath the parent canopy ("dispersal failure"). Large-seeded plants are more prone to dispersal failure, as fewer species of animals are capable of dispersing the seeds, and human impacts decimate large frugivores more often than small frugivores. Following the arrival of humans in New Zealand, a number of large frugivorous birds were driven to extinction. The New Zealand pigeon (kereru, *Hemiphaga novaeseelandiae*, Columbidae) is the sole remaining widespread frugivore that is capable of swallowing and dispersing large-seeded species. The dispersal of large-seeded trees is under threat as kereru numbers have declined due to illegal hunting, habitat loss, and introduced mammalian predators.

I investigated the consequences of dispersal failure for the large-seeded tree species taraire (*Beilschmiedia tarairi*, Lauraceae) and karaka (*Corynocarpus laevigatus*, Corynocarpaceae) in New Zealand. I compared seed predation, germination, seedling

height and survival for dispersed and undispersed seeds for up to two years in the field. I compared the fate of seeds under conspecific adults ("parents") and 20 m away from the parent, whole fruits vs. hand-cleaned seeds, seeds at high vs. low density, and seeds enclosed in mammal-proof cages vs. uncaged seeds in a full factorial design. I analysed data at each recruitment stage using generalised linear mixed effects models.

Taraire seed predation was significantly higher for whole fruits (mean 27%) than hand-cleaned seeds (14%) and for uncaged seeds (30%) compared to caged seeds (10%). For unpredated taraire seeds, fruit pulp removal increased germination success from 84% to 95%. For taraire seeds that germinated, seedling survival after one year was lower for those from whole fruits (7%) than from hand-cleaned seeds (15%), at low density (7%) than high density (15%), underneath parents (7%) than away (16%), and outside cages (10%) compared to inside cages (12%). The combined cumulative effects of dispersal failure and introduced mammals decreased taraire survival after one year from 15% for dispersed seeds protected from mammals to 2% for undispersed seeds with access by mammals (an 87% reduction).

Karaka seed predation was higher for whole fruits (30%) than processed seeds (21%), under parents (30%) than away (21%), and outside cages (34%) than inside cages (17%). For unpredated karaka seeds, germination success was lower under parents (83%) compared to 20 m away (94%). For karaka seeds that germinated, seedling survival to one year was lower for seeds at high density (63%) than low density (70%), outside cages (55%) than inside cages (78%), and under parents (50%) than away (82%). I removed cages from karaka seedlings after one year to allow unrestricted seedling growth. Karaka seedling recruitment from one to two years was lower at high density (63%) than low density (81%) and under parents (57%) compared to 20 m away (81%). Combined cumulative effects of dispersal failure and introduced mammals decreased karaka survival after two years from 60% for dispersed seeds to 11% for undispersed seeds (an 82% reduction). Hence, the effects of kereru seed dispersal persist beyond the dispersal and germination stages. Both dispersal failure and introduced mammals have negative consequences for the regeneration of taraire and karaka in New Zealand forests, in combination reducing surviving seedling numbers by more than 80%.

5.2 Introduction

Global declines in biodiversity threaten to disrupt key ecological processes, including plant-animal mutualisms (e.g. Bond & Slingsby 1984; Aizen & Feinsinger 1994; Robertson et al. 1999; Riera et al. 2002; Sekercioglu et al. 2004). Animal mutualists may persist following anthropogenic disturbance, but in insufficient numbers to carry out their ecological role effectively (McConkey & Drake 2002). There is a growing realisation that maintaining species interactions is as important as conserving the species themselves (Janzen 1974; Fisher 1998; Sekercioglu et al. 2004).

Animal seed dispersers contribute to the maintenance of biodiversity through their role in plant population and community dynamics, gene flow and genetic structure, metapopulation dynamics, and species colonisation rates (Gibson & Wheelwright 1995; Clark et al. 1998b; Hamilton 1999; Christian 2001; Godínez-Alvarez et al. 2002; Purves & Dushoff 2005). A decline in, or loss of, frugivorous animal populations can disrupt seed dispersal mutualisms (Bond & Slingsby 1984; Chapman & Chapman 1995; Traveset 1995; McConkey & Drake 2002). When seed dispersal mutualists are lost and their services are not replaced, seeds remain undispersed and fall beneath the parent canopy ("dispersal failure") (Bond 1994). However, few studies have established that the loss of a single species of seed disperser leads to dispersal failure (Bond & Slingsby 1984). Even fewer have demonstrated significant consequences of dispersal failure for plant populations or communities (Christian 2001).

The risk of a plant becoming (locally) extinct following seed dispersal disruption depends on three factors: 1) the probability of dispersal failure; 2) the plant's reproductive dependence on the seed dispersal mutualism; and 3) its demographic dependence on seeds (Bond 1994). The relationship between fleshy-fruited plants and their animal seed dispersers was originally assumed to be an obligate mutualism, in which passage of seeds through the dispersers gut was required for seeds to germinate. The best-known and still-cited example is the tambalacoque tree and the extinct dodo in Mauritius (Temple 1977). However, subsequent evidence of tambalacoque germination without gut passage or seed abrasion shows that this appealing example is invalid (Witmer & Cheke 1991).

The extent to which dispersers are ecologically redundant will affect how much their disappearance may alter plant populations and communities (Christian 2001; Loiselle & Blake 2002). If multiple dispersers are performing the same ecological role, dispersal failure is less likely (Loiselle & Blake 2002). However, if a more specialised disperser is

lost other frugivores may be unable to provide effective dispersal services. Large-seeded species are more vulnerable to dispersal disruption than small-seeded species, as fewer animal species are large enough to swallow and disperse large seeds (Wheelwright 1985; Clout & Hay 1989; Kitamura et al. 2002). In addition, large-bodied frugivores are devastated by human impacts more often (Cardillo et al. 2005).

Insufficient frugivore activity can limit plant recruitment directly through dispersal limitation—a failure to disperse seeds to potential recruitment sites (Schupp et al. 2002). Dispersal limitation can occur when few seeds are dispersed, many seeds are dispersed short distances, and/or seeds are deposited very patchily (Schupp et al. 2002). Frugivores can also influence plant recruitment indirectly when dispersal limitation means seeds end up at sites where environmental conditions are unsuitable for establishment (Clark et al. 1998a; Schupp et al. 2002).

A number of mechanisms may contribute to decreased survival of undispersed seeds. Frugivore gut passage may enhance germination success through scarification of the seed coat and removal of the fruit pulp (Traveset & Verdú 2002; Robertson et al. 2006). The Janzen-Connell model (Janzen 1970; Connell 1971) proposes that host-specific predators and herbivores maintain high levels of tropical tree diversity through density and/or distance dependent effects. In such cases, seed and/or seedling mortality is predicted to decrease with increasing distance from adult conspecifics.

In this chapter, I investigate the consequences of dispersal failure for regeneration of large-seeded trees in New Zealand. Following the arrival of humans in New Zealand, a number of large frugivorous birds were driven to extinction. Kereru (the New Zealand pigeon, *Hemiphaga novaeseelandiae*, Columbidae) are the sole remaining widespread, native frugivore capable of swallowing and dispersing large-seeded (fruits >14 mm diameter) species. Other native birds capable of dispersing large seeds are either extinct or have a very restricted distribution (Clout & Hay 1989). Five large-seeded tree species (excluding *Beilschmiedia tawaroa*, which is not widely accepted as a separate species) in New Zealand now depend almost entirely on kereru for seed dispersal (Clout & Hay 1989). Declines in kereru populations due to hunting, habitat loss, and introduced mammalian predators (Clout et al. 1995a; Clout et al. 1995b; James & Clout 1996) threaten to disrupt this seed dispersal mutualism. However, the consequences of any loss of seed dispersal service for plant populations and communities are unknown.

I also investigated the role of introduced mammals in limiting the recruitment of large-seeded species. The only extant species of native terrestrial mammals in New

Zealand are two bat species. However, numerous mammal species have been introduced both deliberately and accidentally, including omnivorous possums (*Trichosurus vulpecula*), rats (*Rattus spp.*), mice (*Mus musculus*), goats (*Capra hircus*), and deer (*Cervus elaphus scoticus*). Introduced mammals not only reduce kereru numbers through predation of eggs, chicks and adults (Clout et al. 1995b; Pierce & Graham 1995), but may also limit plant recruitment by preventing seed production (Cowan & Waddington 1990; Cowan 1991; Clout et al. 1995b; Dijkgraaf 2002), destroying seeds (Beveridge 1964; Daniel 1973; Campbell & Atkinson 2002), and browsing on seedlings and saplings (Nugent et al. 2001; Wilson et al. 2003).

The aim of this study was to determine the importance of seed dispersal and introduced mammals to early recruitment stages of the kereru-dispersed, large-seeded tree species karaka (*Corynocarpus laevigatus* J.R.Forst. & G.Forst., Corynocarpaceae) and taraire (*Beilschmiedia tarairi* (A.Cunn.) Benth. & Hook.f. ex Kirk, Lauraceae). These are the two largest-fruited species in the native flora (Wotton & Ladley in press), and as such may be among the most susceptible to dispersal failure. I asked whether post-dispersal seed predation, germination, or seedling survival and growth in karaka and taraire were affected by (1) movement away from parent plants, (2) seed density, (3) pulp removal, or (4) exclusion of introduced mammals.

5.3 Methods

5.3.1 Study organisms

Kereru are large (c. 650 g; Clout & Tilley 1992) fruit pigeons endemic to New Zealand. Although kereru are still widespread throughout New Zealand, their numbers have declined drastically since humans arrived in New Zealand. In some areas of the far north of New Zealand (the centre of diversity for large-seeded tree species) kereru are virtually absent, and they have become locally extinct on Raoul Island (Clout et al. 1995b).

Taraire is a canopy tree that grows up to 20 m or more tall and is found in lowland and coastal forest from the north of the North Island to latitude 38° S (Allan 1961). Taraire drupes are dark purple (19 x 32 mm) with a single seed measuring 16 x 29 mm (Figure 5.1a; Wotton & Ladley in press). Taraire fruits are important in the diet of kereru, particularly as they ripen in winter when few other fruits are available (McEwen 1978). In

many areas there appears to be little or no regeneration of taraire seedlings under a taraire canopy (Dawson & Sneddon 1969).

Karaka is a canopy tree that grows up to 20 m tall and occurs naturally in the northern North Island of New Zealand. The bright orange drupes of karaka measure 20 x 28 mm and contain a single seed 16 x 25 mm (Figure 5.1b; Wotton & Ladley in press). Karaka was cultivated by Maori, and now occurs as far south as Banks Peninsula in the South Island of New Zealand. In apparent contrast to taraire, dense carpets of karaka seedlings are often found beneath karaka trees, indicating some survival without dispersal, at least to the early seedling stage. Karaka has become invasive in some areas outside of its natural range and outcompetes other canopy species (Costall et al. 2006).

5.3.2 Study sites

I conducted research at two sites in New Zealand, Wenderholm Regional Park, near Auckland (36° 32′ S 174° 42′ E) and Mt Tiger Bush, Whangarei (35° 43′ S 174° 23′ E) from January 2005 to February 2007. Wenderholm contains a 55-ha remnant of native lowland podocarp-broadleaf forest ranging in altitude from sea level to 100 m. The forest at Wenderholm is dominated by taraire, karaka, kohekohe (*Dysoxylum spectabile*), and kowhai (*Sophora tetraptera*), with areas of regenerating kanuka (*Kunzea ericoides*) forest. Possum control began at Wenderholm in 1982 and possum numbers have been consistently low since 1994 (Dijkgraaf 2002). Rodent control at Wenderholm began in 1995 and occurs annually (Dijkgraaf 2002).

The Mt Tiger site was located in a 7-ha privately owned block that forms part of the 267-ha Mt Tiger Bush. The site is mainly towai (*Paratrophis banksii*)-dominant secondary lowland forest, ranging in altitude from 140–270 m. During this study, intensive possum and rat control was confined to one area of the site (where two karaka "parents" and three taraire "parents" were located — see below for details), and was carried out from late winter to late summer (R. J. Pierce, personal communication). There was no pest control in the rest of the study site, although it would have gained a slight benefit from the intensive control nearby (R. J. Pierce, personal communication). Feral goats were present in the area during the study and some individuals were killed at the site.

5.3.3 Experimental design

I conducted a field experiment to compare the fate of dispersed and undispersed seeds of karaka and taraire. I used a split-plot full-factorial design with four treatments, each with

two levels: (1) under a conspecific adult (hereafter referred to as the parent) or 20 m away, (2) whole fruits or seeds with the pulp removed, (3) high or low seed density (20 or 4 seeds respectively), and (4) mammal exclusion or open access. Each parent tree was paired spatially with a location 20 m away. Fruit, density and exclusion treatments were nested within parent tree, with plots under and away from parents. I used a distance of 20 m for "away" plots as I was unable to obtain sufficient replicates using greater distances without coming within the radius of another conspecific tree. Previous studies indicate that most parental effects on recruitment are negligible beyond 20 m (Augspurger 1983; Howe et al. 1985; Schupp 1992).

To prevent seeds rolling away I used 7 cm wide strips of lexan polycarbonate (1 mm thick) with the ends stapled together to construct 20 cm diameter tubes. Tubes were inserted into the soil approximately 1 m apart with around 5 cm of the tube remaining above ground (Figure 5.1b). I constructed 30 cm high mammal-proof cages using 5.8 mm aperture stainless steel weldmesh (Figure 5.1c). Cages and tubes were secured to the ground with wire pegs. I randomly assigned each of the eight treatment combinations to each tube in the plot.

This design was replicated at five parent trees at both Wenderholm and Mt Tiger for karaka, and at Mt Tiger for taraire. I initially planned to conduct the experiment for both species at both sites, but the taraire fruit crop virtually failed in 2005. At Mt Tiger I was able to collect taraire fruits from a nearby site to set up the experiment in September 2005. All karaka parent trees at Mt Tiger were fruiting at the start of the experiment in February 2005, but only some parent trees at Wenderholm.

I was unable to locate a number of seeds that were removed from tubes in the karaka experiment. Because the karaka experiment was set up earlier, I was able to modify the experiment for taraire. I therefore marked taraire fruits and seeds to increase the recovery rate and help determine their fate (Figure 5.1d). I tagged seeds by tying one end of a 15 cm length of nylon fishing line to 5 cm strips of pink and black striped flagging tape, and gluing the other end to the seed. I cut the flagging tape to a point at the end attached to the nylon line to decrease snagging and numbered each tag to aid identification. I conducted a pilot study in June 2005 at Wenderholm to determine whether tagging affected taraire seed removal rates. I placed either four hand-cleaned seeds or four whole fruits in each tube. Half of the tubes had tagged seeds and the other half were untagged. I repeated this at two locations at Wenderholm (giving two replicates for each treatment combination) and recorded removal rates after one month. Removal of tagged and

untagged seeds did not differ, and I therefore assumed that marking of seeds had no effect on seed removal.

I monitored karaka seeds one week after setting up the experiment, monthly for the first six months, and then at one and two years. Taraire seeds were monitored monthly for the first three months and then at one year. I placed any litter found on top of a cage at each visit inside the tube to reduce the effect of interception of litter-fall by cages. At each visit I recorded seed disappearance, insect and mammal predation, germination, seedling height and survival for each seed or seedling. I removed cages from karaka seedlings after one year to allow unrestricted seedling growth.

Insect-eaten seeds were characterised by small holes in the seed or seed coat and the presence of insects and/or frass. Mammal-eaten seeds generally had 2–3 mm wide tooth marks consistent with rodent predation (Beveridge 1964; Dijkgraaf 2002). Some seeds that were partially eaten by either insects or mammals still germinated. Therefore, I classified only those seeds that suffered fatal predation as being eaten, assigning the fate of each seed prior to germination into four unique categories: disappeared, insect-predated, mammal-predated, or uneaten. For some seeds, predation occurred after germination, in which case I classified it as mortality during year one (when fatal). For the purpose of the analysis I assumed seeds that disappeared were killed as I found no evidence of seed caching (c.f. Vander Wall et al. 2005). A small number of seeds that were initially classified as disappeared were subsequently located outside the tube, where I continued to follow their fate. I classified seeds as germinated upon radicle emergence. A seed was considered alive if it remained firm, and viable karaka seeds were often green beneath the seed coat.

(a)

(b)

(c)

(d)

Figure 5.1 (a) Taraire (*Beilschmiedia tarairi*) fruits; (b) karaka (*Corynocarpus laevigatus*) fruits in experimental tubes (Photo: Javi Rodríguez); (c) mammal-proof cage covering karaka seedlings; (d) taraire seeds and fruits were marked with strips of pink and black striped flagging tape tied to fluorescent yellow nylon fishing line, which was attached to the seed with super glue.

5.3.4 Statistical analysis

I analysed data at each stage of recruitment, i.e. total seed predation (including insect predation, mammal predation, and removed seeds), germination of those seeds that were not eaten, survival and growth to one year for germinated seeds, and survival and growth from one to two years for those seedlings alive after one year. I used generalised linear mixed models (GLMMs) to analyse seed predation, germination, and seedling survival (the binomial response variables) for each species. GLMMs provide a framework for analysing data with a non-normal error distribution and hierarchical random effects. I used linear mixed models (LMMs) to analyse seedling growth for one and two years for karaka and for one year for taraire. For seed predation, germination, and seedling survival GLMMs I specified a binomial error distribution (and associated logit link), with number of successes/number of failures as the response variable. For seedling growth LMMs I specified a Gaussian error distribution.

For seed predation, one-year seedling survival, and one-year seedling height, I constructed a (maximal) model that initially included all explanatory variables (location, density, fruit, and mammal exclusion) and all two-way interactions as fixed effects. For germination I included location, density, and fruit and all two-way interactions as fixed effects in the maximal model. For karaka two year seedling survival and growth, I included location, density, and cage and the two-way interactions between the three variables as fixed effects. I included plots nested within parent trees as random effects in all models. For karaka models, I also included site as a fixed effect in the maximal model, analysing data for the two sites separately when site had a significant effect.

I fitted the GLMMs using Laplacian approximation to maximum likelihood and the LMMs using restricted maximum likelihood. I used model simplification by backward selection to construct final models. I compared the effect of removing each variable from the maximal model on Akaike Information Criterion (AIC) values. AIC provides a measure of model fit accounting for the sample size and the number of parameters estimated in the model, with smaller values of AIC indicating a better-fitting model. I proceeded with simplification of the model with the lowest AIC value until removing any variable increased the AIC value. I calculated ΔAIC as the difference in AIC between a model and the best-fitting (final) model, which has ΔAIC of 0. As a rule of thumb, models with $\Delta AIC \leq 2$ have substantial support, those with $4 \leq \Delta AIC \leq 7$ weaker support, and those with $\Delta AIC > 10$ virtually no support (Burnham & Anderson 2001). Where multiple

models had $\Delta AIC \leq 2$, I selected the model with the lowest AIC value as the final model, except where interaction terms in that model appeared biologically insignificant from graphical inspection of the data. I ran all models using the lme4 package in R version 2.4.1 (R Development Core Team 2006).

5.4 Results

5.4.1 Secondary dispersal and seed predation

Karaka fruit pulp was eaten by both insects and mammals (Figures 5.2a and 5.2b). Insects consumed the pulp over many months, while mammals ate the pulp within one month, sometimes depositing the unharmed seeds outside tubes (Figure 5.2b). Some seeds where mammals ate the pulp were subsequently predated by mammals or disappeared. Other seeds were moved outside tubes without the pulp or seed being eaten. Most of these seeds, mammal-predated seeds, and tags from seeds that disappeared (hereafter referred to as removed) were recovered within 1 m of the tube and I found no evidence of seed caching. For taraire, tags were recovered from a mean of 70 % of removed seeds.

Both insects and mammals ate karaka and taraire seeds (Figures 5.2c–5.2f and 5.3). Insect predators found in karaka seeds were identified as the Lepidopteran larvae *Cryptaspasma querula* (*Tortricidae*) (R. Hoare, personal communication). Mammal seed predation occurred for up to five months after seed sowing, while seeds were removed (and probably eaten by mammals) for up to six months. Cages did not appear to restrict access to seeds by invertebrate seed predators (with the possible exception of weta), and karaka insect predation was higher when seeds were inside cages (Figures 5.3b–5.3d). Protection of seeds from mammals had the greatest effect on seed predation levels for both karaka and taraire, with 30% or more of uncaged seeds eaten (Figure 5.3).

(a)

(b)

(c)

(d)

(e)

(f)

Figure 5.2 Pulp removal and predation of karaka seeds. (a) Insect pulp removal; (b) mammal pulp removal and secondary dispersal; (c) karaka seed predation probably by ship rats (d) karaka seed predation probably by possums; (e) entry and exit holes in karaka seed indicating predation typical of unidentified beetle larvae; (f) the same insect-predated seed broken open to reveal frass inside and seed completely eaten.

Seven models of taraire seed predation had substantial support, with $\Delta AIC \leq 2$ (Appendix II). The final model is shown in Table 5.1a. Taraire seed predation was much higher for whole fruits than hand-cleaned seeds and for uncaged seeds compared to caged seeds (Figure 5.3a). Insect predation was higher for whole taraire fruits than hand-cleaned seeds, while mammal predation only occurred outside cages (Figure 5.3a). For whole fruits, predation levels were higher at low density (31%) than at high density (22%), while density had little effect on predation levels for hand-cleaned seeds. Seeds at low density experienced a four-fold increase in predation levels from caged to uncaged treatments, compared to a doubling in predation levels for seeds at high density.

Site was a significant predictor of karaka seed predation, therefore I constructed separate models for each site. At each site, three models for karaka seed predation had substantial support (with $\Delta AIC \leq 2$). The final models for each site are shown in Tables 5.1b and 5.1c. Karaka seed predation was higher outside cages than inside cages at both sites, and higher for whole fruits than processed seeds, and under parents than away at Mt Tiger (Figure 5.3). At Mt Tiger, karaka seeds not protected from mammals had much higher predation levels under parents (53%) than seeds 20 m away (23%), while around 20% of seeds inside cages were eaten regardless of location. The increase in predation levels in whole fruits compared to processed seeds was greater inside cages that outside. At Mt Tiger, insect predation was greater for whole fruits than processed seeds (Figure 5.3c). Insect predation was higher for karaka seeds inside cages than outside, while mammal predation (including removed seeds) was higher for whole fruits than clean seeds, under parents than away, and outside cages than inside (Figure 5.3).

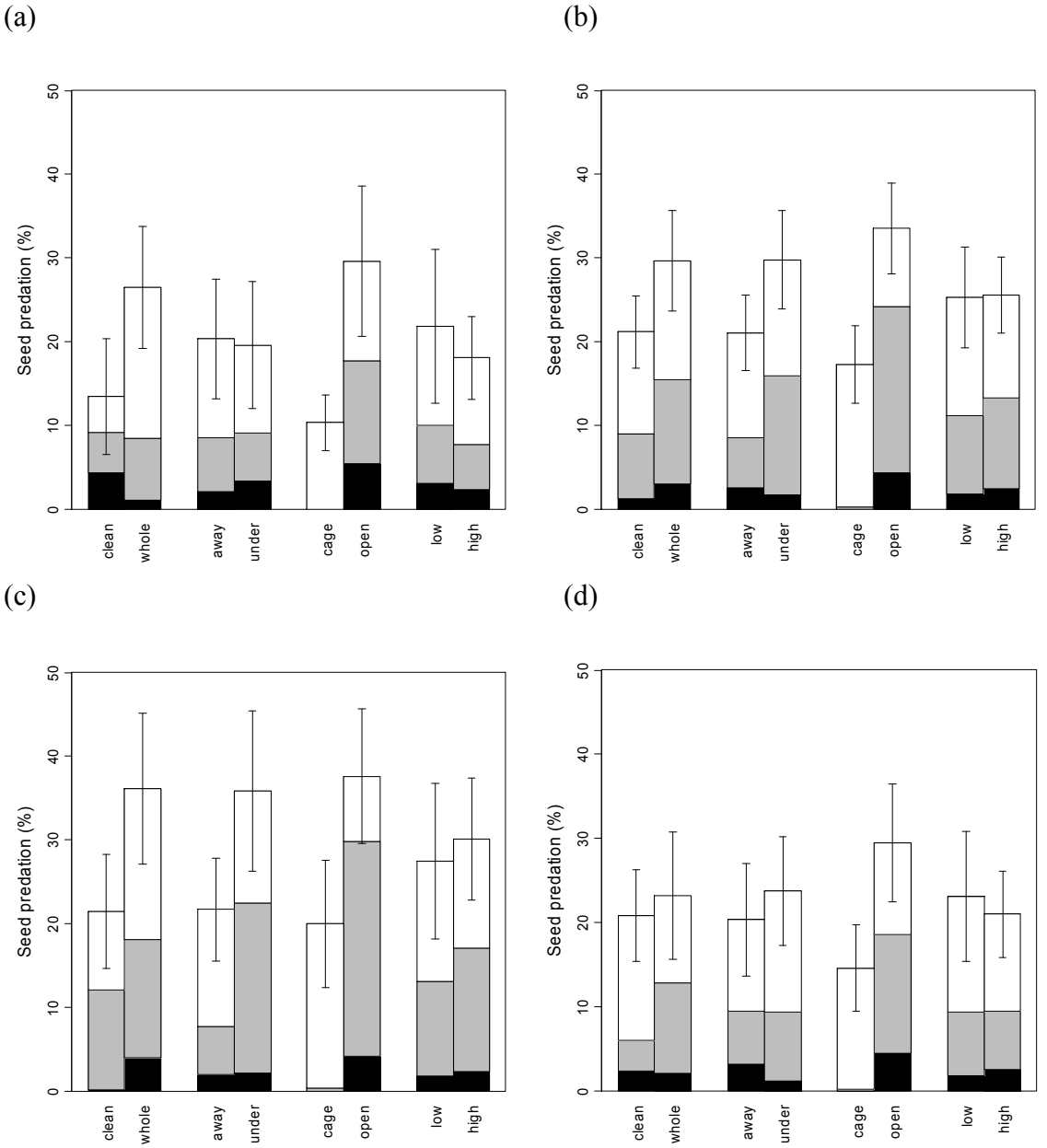


Figure 5.3 Main treatment effects on mean seed predation percentage. Treatments were cleaned seeds vs. whole fruits, 20 m away from "parents" vs. under "parents", mammal exclusion vs. open access, low seed density (4 seeds) vs. high seed density (20 seeds). White = insect predation, grey = removed, black = mammal predation. Error bars are 95% confidence intervals. (a) taraire, (b) karaka at both sites, (c) karaka at Mt Tiger, (d) karaka at Wenderholm.

Table 5.1 Total seed predation (insect, mammal, and removed seeds) parameter estimates and standard errors (s.e.) from GLMMs for (a) taraire (*Beilschmiedia tarairi*), (b) karaka (*Corynocarpus laevigatus*) at Mt Tiger, and (c) karaka at Wenderholm. For each response variable only the final model is shown.

(a) Taraire

parameter	level	estimate	s.e.
intercept		– 2.65	0.34
fruit	whole fruit	1.08	0.37
density	low	– 0.99	0.59
cage	uncaged	1.16	0.31
location	under	0.25	0.36
fruit:density	whole:low	0.87	0.49
fruit:cage	whole:uncaged	– 0.46	0.38
fruit:location	whole:under	– 0.54	0.35
density:cage	low:uncaged	1.05	0.53

(b) Karaka at Mt Tiger

Parameter	level	estimate	s.e.
intercept		– 1.93	0.28
fruit	whole fruit	1.25	0.25
cage	uncaged	0.40	0.30
location	under	– 0.49	0.33
fruit:cage	whole:uncaged	– 0.73	0.33
cage:location	uncaged:under	2.03	0.32

(c) Karaka at Wenderholm

parameter	level	estimate	s.e.
intercept		– 1.82	0.16
cage	uncaged	0.87	0.17

5.4.2 Germination of unpredated seeds

Taraire seeds germinated within one to three months of sowing, and any ungerminated seeds were soft by three months. Overall, 72% of taraire seeds germinated. Three taraire germination models had substantial support ($\Delta AIC \leq 2$) and the final model is shown in Table 5.2a. For taraire seeds, germination success was higher for hand-cleaned seeds than whole fruits (Figure 5.4a). For hand-cleaned seeds, germination success was greater at low density (98%) than high density (92%), which was reversed for whole fruits where germination success was greater at high density (88%) than low (79%).

Karaka seeds started germinating one month after sowing. Most karaka seeds germinated between four to six months after sowing, but a small number germinated after one year. Overall, 67% of karaka seeds germinated. Site had a significant effect on variation in karaka germination. At Mt Tiger, five models had substantial support, with $\Delta AIC \leq 2$. At Wenderholm, four models had substantial support. The final models for each site are shown in Tables 5.2b and 5.2c. For karaka seeds, germination success was lower under parents compared to 20 m away (Figures 5.4b–5.4d). The effect of location on germination success was greater at Mt Tiger than Wenderholm.

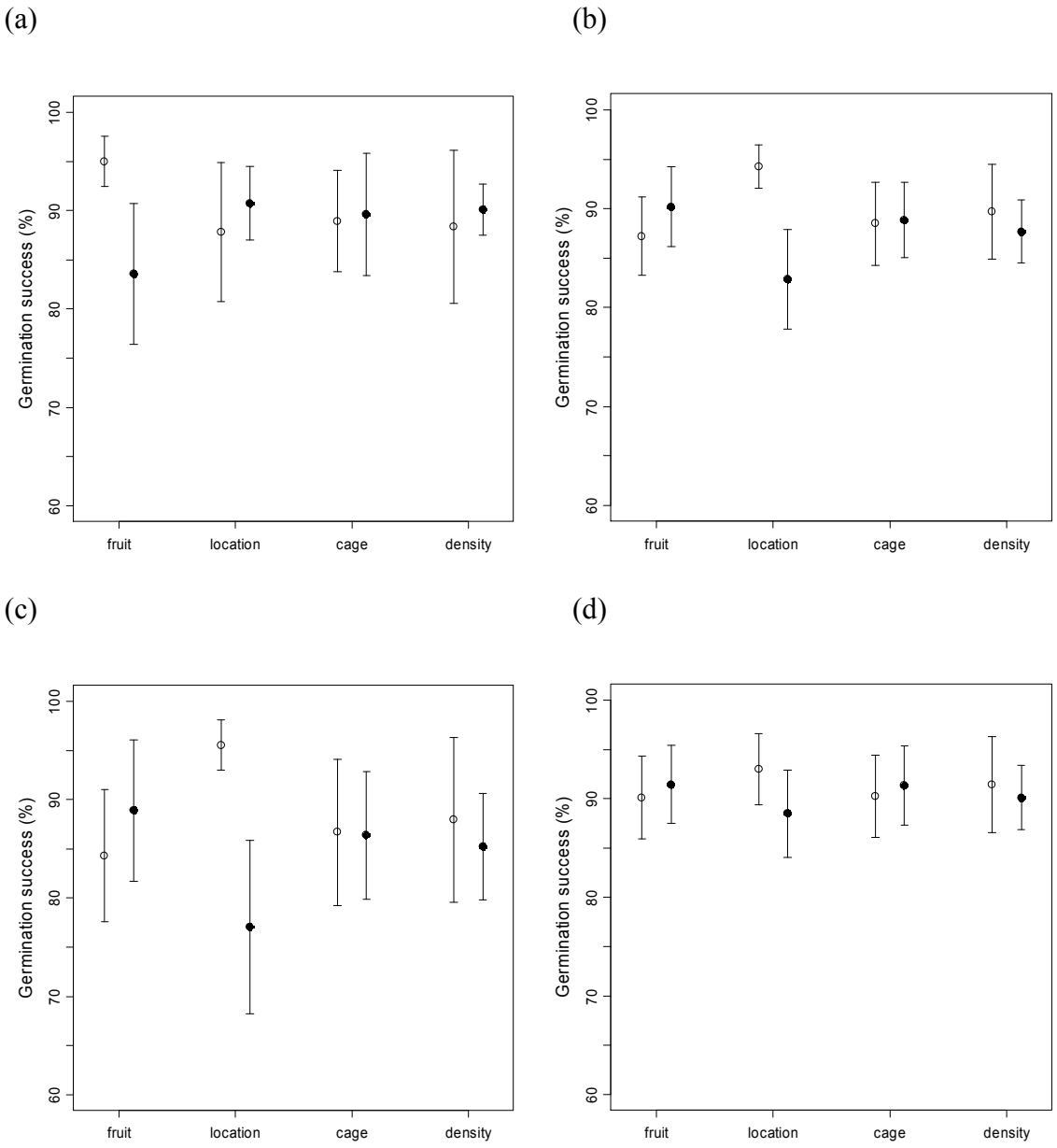


Figure 5.4 Main treatment effects on mean germination success for (a) taraire, (b) karaka at both sites, (c) karaka at Mt Tiger, and (d) karaka at Wenderholm. Open circles represent pre-human treatment levels (processed seeds, 20 m away, caged, and low density), while filled circles represent post-human treatment levels (whole fruits, under parents, uncaged, and high density). Error bars are 95% confidence intervals.

Table 5.2 Germination success (for unpredated seeds) parameter estimates and standard errors (s.e.) from GLMMs for (a) taraire (*Beilschmiedia tarairi*), (b) karaka (*Corynocarpus laevigatus*) at Mt Tiger, and (c) karaka at Wenderholm. For each response variable only the final model is shown.

(a) Taraire

parameter	level	estimate	s.e.
intercept		2.62	0.30
fruit	whole fruit	– 0.36	0.26
density	low	1.33	1.05
location	under	– 0.37	0.35
fruit:density	whole:low	– 2.55	1.09
density:location	low:under	1.21	0.73

(b) Karaka at Mt Tiger

parameter	level	estimate	s.e.
intercept		2.94	0.32
fruit	whole fruit	0.07	0.26
density	low	0.01	0.42
location	under	– 1.76	0.37
fruit:density	whole:low	1.25	0.88

(c) Karaka at Wenderholm

parameter	level	estimate	s.e.
intercept		2.88	0.40
location	under	– 0.69	0.55

5.4.3 Seedling survival and growth

I observed both insect and mammal herbivory of karaka seedlings (Figure 5.5). Taraire seedlings were not attacked by insects, although some were browsed by mammals.

Figure 5.5 Insect herbivory of karaka seedlings.

Six models of taraire seedling survival to one year had substantial support (Appendix II) and the final model is shown in Table 5.3a. For taraire seeds that germinated, seedling survival after one year was lower for those from whole fruits than from hand-cleaned seeds, at low density than high density, and underneath parents than away (Figure 5.6a). Inside cages, taraire seedling survival was greater at high density (20%) than at low density (5%), while outside cages survival was around 10% at both high and low density.

Site had a significant effect on variation in karaka survival to one year. For each site, five models for survival to one year had substantial support (Appendix II). The final models for each site are shown in Tables 5.3b and 5.3c. For karaka seeds that germinated, seedling survival to one year was lower for seeds at high density than low density, outside cages than inside cages, and under parents than away (Figures 5.6b–5.6d).

Three models for karaka survival through the second year had substantial support (Appendix II). Karaka seedling recruitment from one to two years was lower at high density than low density and under parents compared to 20 m away (Figure 5.7). Density-dependent effects were greater underneath parents with 48% survival at high density

compared to 71% at low density. At locations 20 m away survival was 75% and 87% at high and low density respectively.

Eight models for taraire seedling growth during year one had substantial support (Appendix II) and the final model is shown in Table 5.4a. Taraire seedling height after one year was greater inside cages than outside (Figure 5.8a). Uncaged seedlings were taller at low density than high, while there was no effect of density for caged seedlings (Table 5.4a). While taraire seedling growth was always greater for hand-cleaned seeds than whole fruits, the difference was greater under parents than 20 m away (Table 5.4a).

Site had a significant effect on variation in karaka seedling growth during both years. For each site, three models for growth during year one had substantial support (Appendix II) and the final models are shown in Tables 5.4b and 5.4c. Karaka seedling growth during the first year was lower under parents than 20 m away at both sites (Figures 5.8 b–5.8d; Tables 5.4b and 5.4c). At Mt Tiger, seedling growth for whole fruits was greater in cages than in the open, while there was no difference for processed seeds. At Wenderholm, seedling growth at high density was greater away from parents than under.

Three models of karaka growth during year two for Mt Tiger, and two models for Wenderholm had substantial support (Appendix II) and the final models are shown in Tables 5.4b and 5.4c. Karaka seedling growth during the second year was greater for caged seedlings than uncaged seedlings and away from parents than under at both sites (Figure 5.9). Note that the cages had been removed by this time, but continued to have an effect (just as pulp removal was still having an effect on taraire survival well after germination). At Wenderholm, seedling growth was greater for seedlings at high density than low.

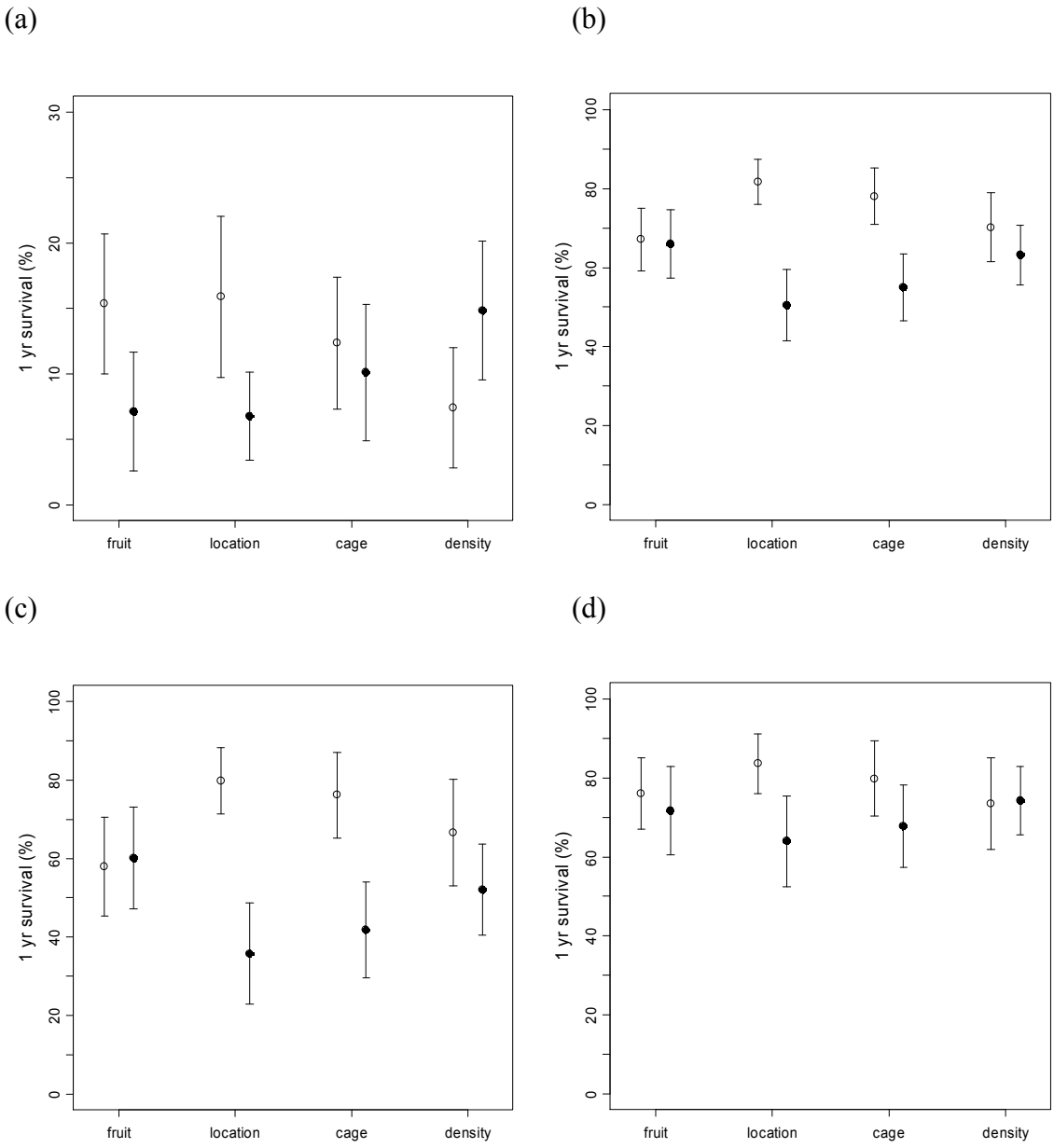
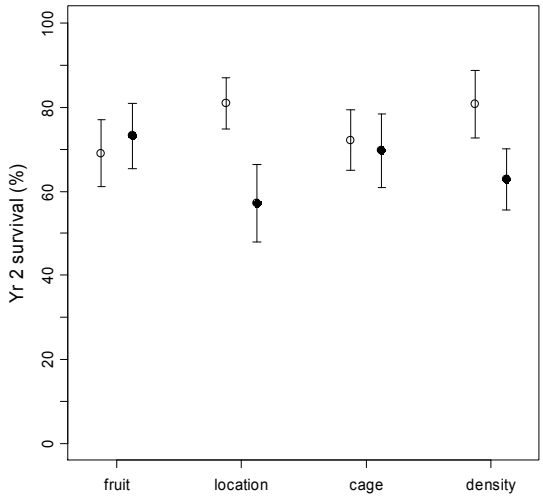


Figure 5.6 Main treatment effects on mean survival to one year for (a) taraire, (b) karaka at both sites, (c) karaka at Mt Tiger, and (d) karaka at Wenderholm. Open circles represent pre-human treatment levels (processed seeds, 20 m away, caged, and low density), while filled circles represent post-human treatment levels (whole fruits, under parents, outside cages, and high density). Error bars are 95% confidence intervals. Note the different y-axis scale in graph (a).

(a)



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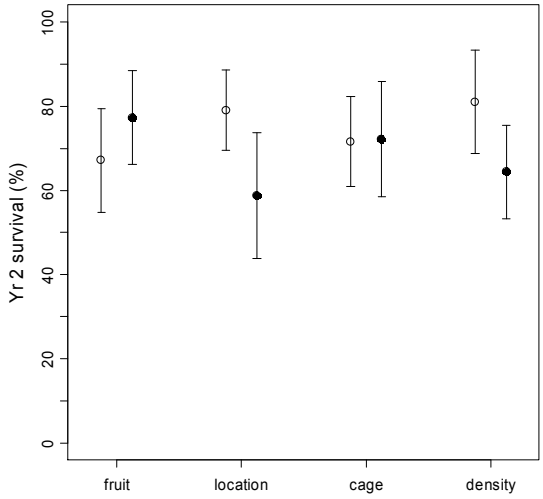

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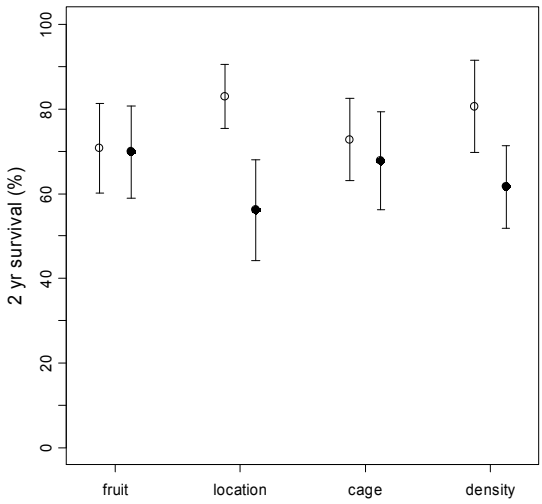


Figure 5.7 Main treatment effects on mean survival through the second year for karaka at (a) both sites, (b) Mt Tiger, and (c) Wenderholm. Open circles represent pre-human treatment levels (processed seeds, 20 m away, caged, and low density), while filled circles represent post-human treatment levels (whole fruits, under parents, outside cages, and high density). Error bars are 95% confidence intervals.

Table 5.3 Survival of germinated seeds to one year parameter estimates and standard errors (s.e.) from GLMMs for (a) taraire (*Beilschmiedia tarairi*), (b) karaka (*Corynocarpus laevigatus*) at Mt Tiger, and (c) karaka at Wenderholm, and (d) survival of karaka seedlings from one to two years at both sites (data for both sites were combined as site was not significant in the final model). For each response variable only the final model is shown.

(a) Taraire

parameter	level	estimate	s.e.
intercept		– 0.76	0.42
fruit	whole fruit	– 0.49	0.28
density	low	– 1.50	0.55
cage	uncaged	– 0.97	0.29
location	under	– 1.13	0.62
fruit:location	whole:under	– 0.99	0.55
density:cage	low:uncaged	1.49	0.74
cage:location	uncaged:under	0.73	0.48

(b) Karaka at Mt Tiger

parameter	level	estimate	s.e.
intercept		2.03	0.46
fruit	whole fruit	1.36	0.52
density	low	0.74	0.29
cage	uncaged	– 1.89	0.30
location	under	– 2.16	0.60
fruit:cage	whole:uncaged	– 0.90	0.54
fruit:location	whole fruit:under	– 1.04	0.54

Table 5.3 cont.

(c) Karaka at Wenderholm

parameter	level	estimate	s.e.
intercept		2.25	0.42
fruit treatment	whole fruit	1.09	0.44
density	low	– 0.48	0.42
cage	uncaged	– 0.32	0.29
location	under	– 1.25	0.53
fruit:cage	whole:uncaged	– 1.17	0.42
fruit:location	whole fruit:under	– 1.00	0.44
density:location	low:under	0.87	0.55

(d) Karaka at both sites

parameter	level	estimate	s.e.
intercept		1.25	0.30
density	low	0.82	0.23
location	under	– 1.20	0.43

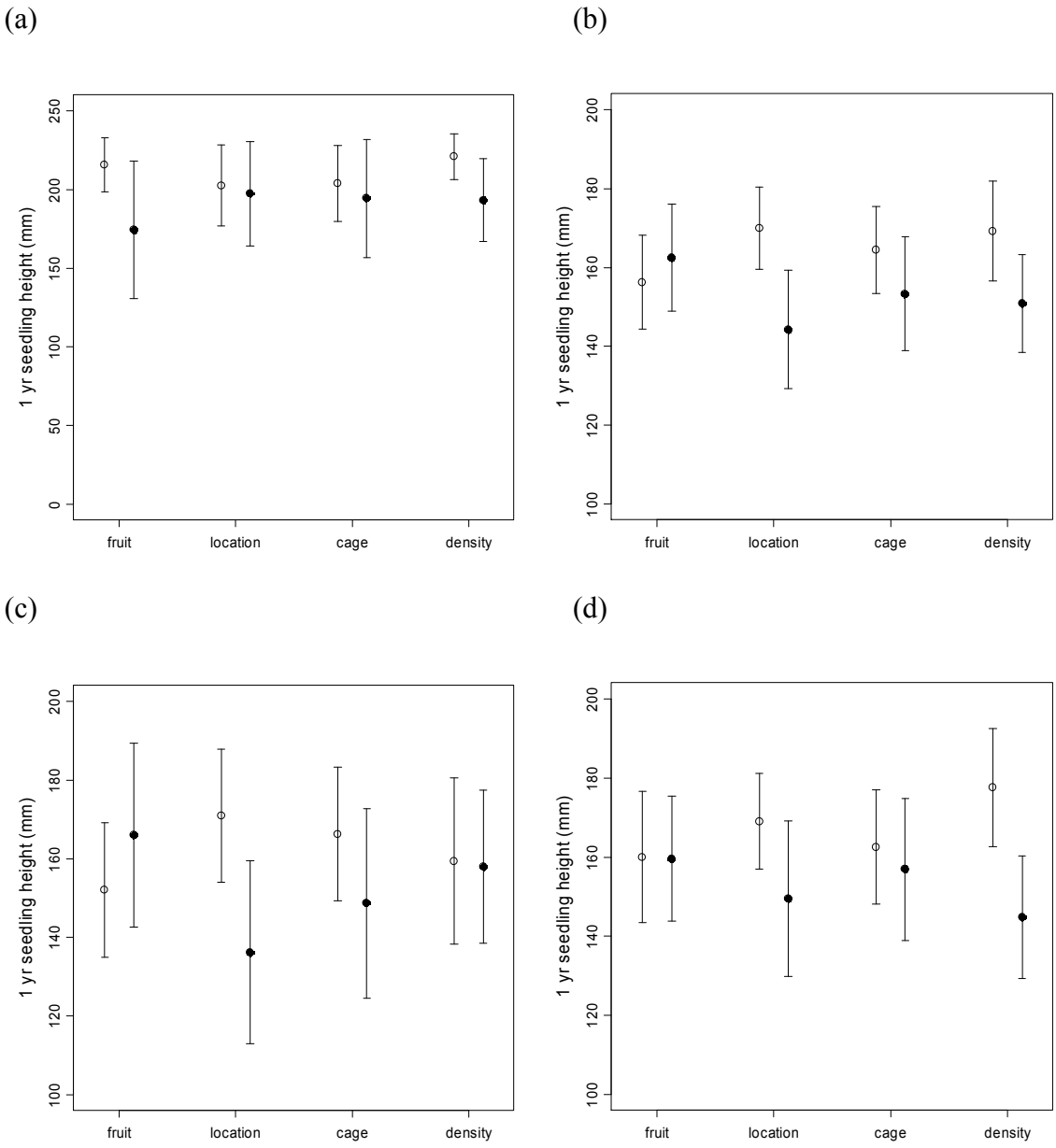
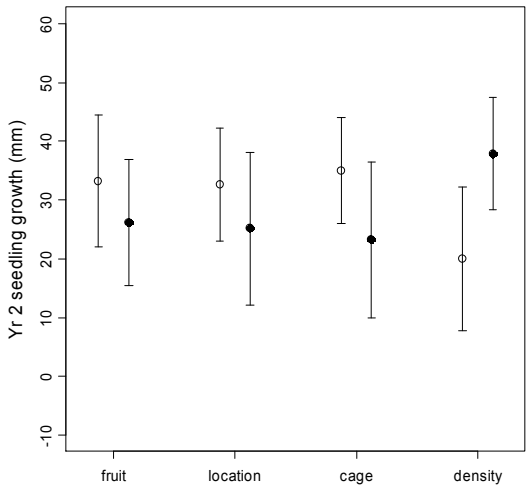


Figure 5.8 Main treatment effects on mean seedling height (mm) at one year for (a) taraire, (b) karaka at both sites, (c) karaka at Mt Tiger, and (d) karaka at Wenderholm. Open circles represent pre-human treatment levels (processed seeds, 20 m away, caged, and low density), while filled circles represent post-human treatment levels (whole fruits, under parents, outside cages, and high density). Error bars are 95% confidence intervals.

(a)



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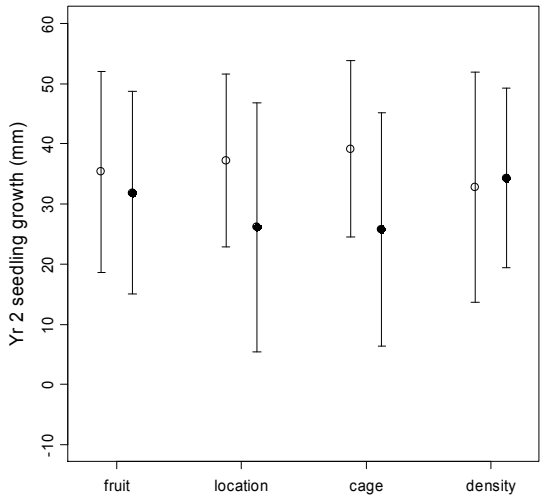

(c)

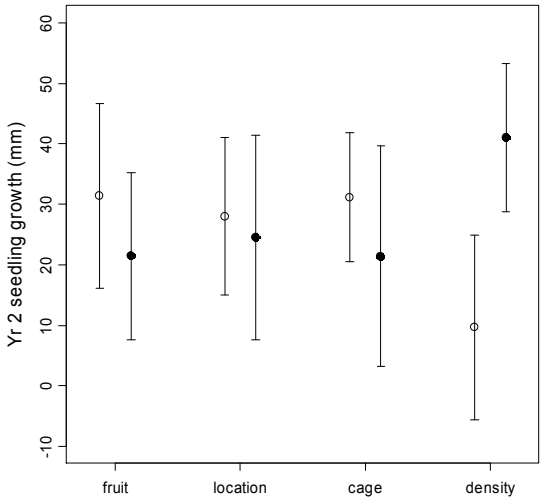

Figure 5.9 Main treatment effects on mean seedling height growth (mm) during year two for (a) karaka at both sites, (b) karaka at Mt Tiger, and (c) karaka at Wenderholm. Open circles represent pre-human treatment levels (processed seeds, 20 m away, caged, and low density), while filled circles represent post-human treatment levels (whole fruits, under parents, outside cages, and high density). Error bars are 95% confidence intervals.

Table 5.4 Seedling height growth parameter estimates and standard errors (s.e.) from GLMMs for (a) taraire (*Beilschmiedia tarairi*), (b) karaka (*Corynocarpus laevigatus*) at Mt Tiger and (c) karaka at Wenderholm. For each response variable only the final model is shown.

(a) Taraire

parameter	level	estimate	s.e.
1 yr growth			
intercept		222.93	24.23
fruit	whole fruit	– 25.31	23.44
density	low	– 18.53	28.69
cage	uncaged	– 49.80	21.13
location	under	9.10	33.54
fruit:location	whole:under	– 57.18	35.79
density:cage	low:uncaged	63.18	40.27

(b) Karaka at Mt Tiger

parameter	level	estimate	s.e.
1 yr growth			
intercept		168.59	16.25
fruit	whole fruit	30.49	16.83
cage	uncaged	– 3.31	17.55
location	under	– 39.86	19.58
fruit:cage	whole:uncaged	– 45.12	25.32
2 yr growth			
intercept		49.75	11.99
cage	uncaged	– 26.39	13.47
location	under	– 24.01	18.50
cage:location	uncaged:under	37.50	25.68

Table 5.4 cont.

(c) Karaka at Wenderholm

parameter	level	estimate	s.e.
1 yr growth			
intercept		162.25	11.12
density	low	13.40	13.46
location	under	– 29.08	16.04
density:location	low:under	28.36	19.86
2 yr growth			
intercept		39.64	9.88
density	low	– 15.55	12.76
cage	uncaged	4.64	12.48
density:cage	low:uncaged	– 29.65	18.39

5.4.4 Overall effects

Seed dispersal had a greater effect than exclusion of introduced mammals on taraire survival during early stages of recruitment. Dispersal failure decreased the probability of taraire survival during the first year by 60% for caged seeds and 73% for uncaged seeds. Fruit pulp removal decreased taraire mortality at all recruitment stages (Table 5.5a; Figures 5.4–5.6). One year after sowing, taraire survival was greater for hand-cleaned seeds (13%) than whole fruits (5%), at high density (12%) than low (6%), inside cages (11%) than outside cages (8%), and away from parents (13%) than under (6%). The combined cumulative effects of dispersal failure and introduced mammals decreased taraire survival after one year from 15% for dispersed seeds protected from mammals to 2% for undispersed seeds with access by mammals (an 87% reduction; Figure 5.10).

Dispersal failure decreased the probability of karaka survival two years after sowing by 62% (inside cages) and 93% (outside cages) at Mt Tiger and 47% (inside cages) and 58% (outside cages) at Wenderholm. For karaka seeds, movement away from the parent had the greatest effect, increasing survival at all recruitment stages (Table 5.5b). Karaka cumulative survival after one year was greater for seeds inside cages (56–65%, Mt Tiger and Wenderholm respectively) than outside (27–47%), and away from parents (59–

65%) than under (24–46%). At Mt Tiger, karaka seeds at low density had greater survival (46%) than at high density (37%), while there was no difference at Wenderholm (56% at both high and low density). Survival was similar for processed karaka seeds (42–57%) and whole fruits (40–55%) at both sites.

After two years, karaka cumulative survival was greater for seeds at low density (36-46%) than high (25–37%), inside cages (41–50%) than outside (21–33%), and away from parents (47–54%) than under (15–29%). Survival was similar for processed karaka seeds (29–44%) and whole fruits (36–39%). Combined cumulative effects of dispersal failure and introduced mammals decreased karaka survival after two years from 50–70% for dispersed seeds in cages to 3–19% for undispersed seeds outside cages (a 73–94% reduction; Figure 5.10). For both taraire and karaka, the survival benefits of dispersal and mammal exclusion were greatest at the seed predation and one year survival stages of recruitment (Table 5.5; Figure 5.10). Seed dispersal had the least effect on germination success.

Table 5.5 Summary of main effects of seed dispersal and mammal exclusion on mean percent change in survival and growth compared to undispersed seeds without mammal exclusion at each recruitment stage. Non-significant effects are indicated by zero. (a) taraire, (b) karaka (where means differ between sites, the first number is for Mt Tiger and the second is for Wenderholm).

(a) Taraire

	% change in mean survival and growth			
recruitment stage	pulp removal	away from parent	caged	low density
predation	+ 18	0	+ 27	– 5
germination	+ 14	0	—	0
survival yr 1	+ 117	+ 134	+ 23	– 50
height yr 1	+ 24	0	0	+ 15

(b) Karaka

	% change in mean survival and growth			
recruitment stage	pulp removal	away from parent	caged	low density
predation	+ 23, 0	+ 22, 0	+ 28, + 21	0
germination	0	+ 24, + 5	—	0
survival yr 1	0	+ 122, + 31	+ 82, + 18	+ 28, 0
survival yr 2	0	+ 35, + 48	0	+ 26, + 31
height yr 1	– 8, 0	+ 25, + 10	+ 12, 0	0, + 19
height yr 2	0	+ 43, + 14	+ 52, + 46	0, – 76

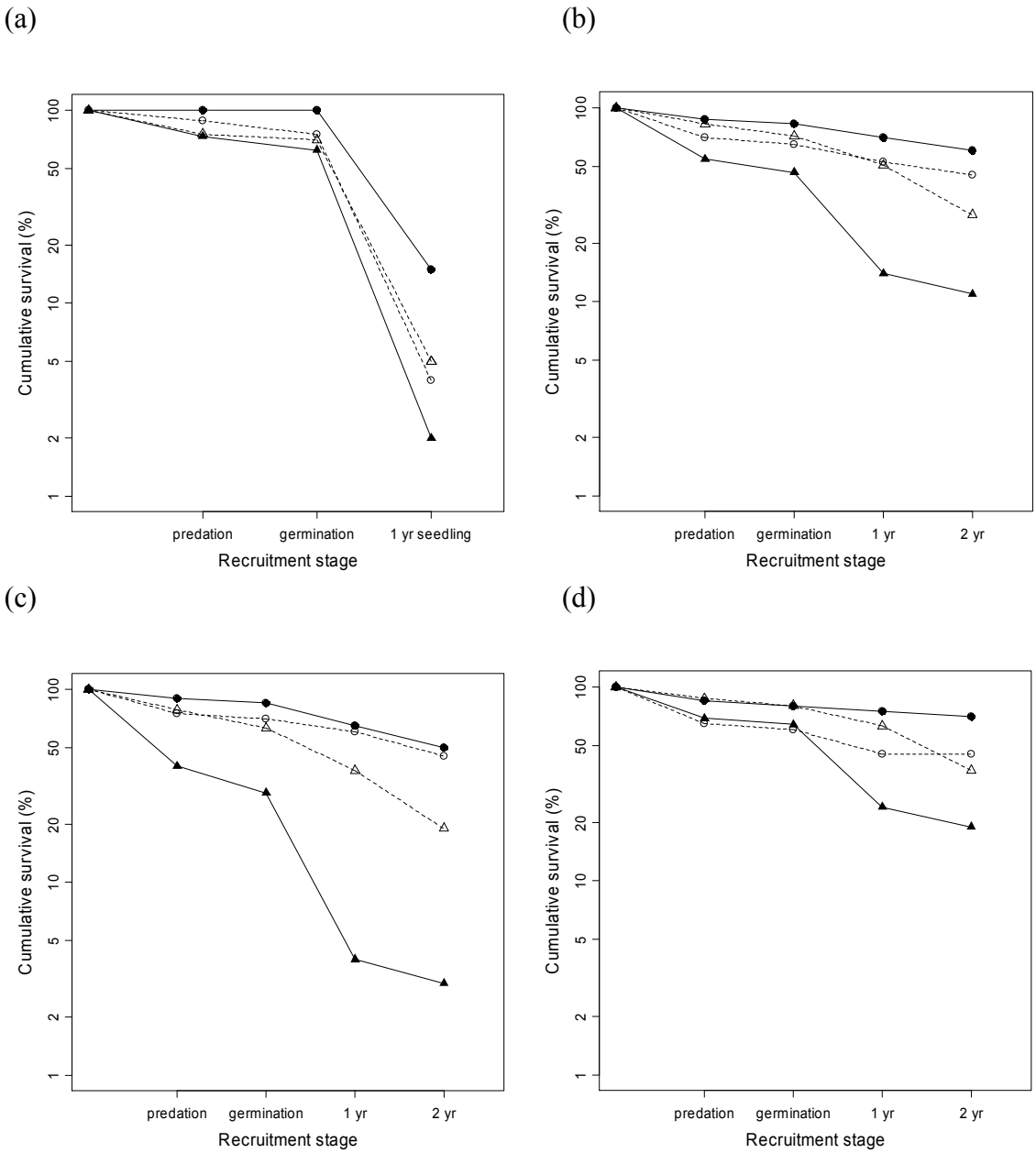

Figure 5.10 Observed mean cumulative survival rates under four scenarios: (1) pre-human (best-case scenario — dispersal of seeds without introduced mammals, represented by filled circles), (2) post-human (worst-case scenario — dispersal failure with mammals, represented by filled triangles), (3) dispersal with mammals (represented by open circles), and (4) dispersal failure without mammals (open triangles). Treatment levels for dispersal are clean seeds, 20 m away from parent, and low density. Treatment levels for dispersal failure are whole fruits, under parents, and high density. (a) taraire, (b) karaka at both sites, (c) karaka at Mt Tiger, (d) karaka at Wenderholm. Note the y-axis log scale.

5.5 Discussion

My results illustrate five main points: (1) Seed dispersal greatly enhanced survival of both karaka and taraire during early recruitment stages; (2) distance- and density-dependent effects both contributed to increased mortality of undispersed taraire and karaka seeds, as predicted by the Janzen-Connell hypothesis (Janzen 1970; Connell 1971); (3) fruit pulp removal increased germination success only for taraire, but decreased seed predation for both species and (surprisingly) taraire seedling mortality; (4) introduced mammals also decreased the probability of recruitment through predation of seeds and seedlings; (5) the combined effects of dispersal failure and introduced mammals could have serious consequences for the regeneration of both taraire and karaka.

5.5.1 Janzen-Connell effects

The Janzen-Connell hypothesis predicts that mortality of seeds and seedlings will decrease with increasing distance from parent trees, due to distance- or density-dependent host-specific enemies (Janzen 1970; Connell 1971). Although a large body of research has been devoted to testing the Janzen-Connell hypothesis in the tropics (e.g. Augspurger 1984; Howe et al. 1985; Schupp 1992; Hyatt et al. 2003), Janzen-Connell effects have rarely been demonstrated in temperate areas (but see Packer & Clay 2000).

I found positive distance-dependent effects on survival in taraire and karaka at multiple recruitment stages (Table 5.5). Several factors are probably responsible for increased mortality under parents in these species. Higher taraire seedling mortality under parents may be due to the deep, persistent litter layer that forms beneath taraire trees, rather than host-specific enemies (Myers 1984). Rodents may use parent trees as signals indicating the presence of juveniles (Janzen 1970). If rodents act as distance responsive predators, searching for seeds should be concentrated on areas around fruiting trees. At Mt Tiger, karaka seeds were more likely to be eaten by mammals (but not insects) when under parents than 20 m away (Figure 5.3; Table 5.1), and parent trees at this site were fruiting heavily when I set up the experiment. This effect was not observed in karaka at Wenderholm or in taraire, where most “parent” trees were not fruiting or produced very few fruits. Host-specific insects feeding in the parent canopy can also act as distance-responsive seedling predators. I observed insect herbivory on karaka seedlings, which suffered higher mortality under parents. Allelopathic effects and pathogens may also have

contributed to lower karaka germination success and higher mortality for either species under parents (Augspurger 1984; Traveset 1998; Packer & Clay 2000).

Density-dependent effects on survival differed between karaka and taraire. The increased germination success of whole taraire fruits at high density compared to low density (Table 5.2a) is contrary to what might be expected. Detrimental pathogens tend to increase at high densities (Janzen 1970), and fruit pulp can become infected with fungi or bacteria that may prevent germination (Traveset 1998). Reduced taraire seed predation and seedling mortality at high density (Table 5.5a) may be due to satiation of mammalian seed predators outside cages and of insect seedling predators inside cages (Janzen 1970). In contrast, karaka seedlings exhibited negative density-dependent mortality (Table 5.5b).

5.5.2 Fruit pulp removal

Fruit pulp removal was more important for decreasing seed predation than increasing germination success, particularly for karaka (Table 5.5). Germination experiments are often conducted under artificial conditions (in glasshouses or laboratories), where the breakdown of fruit pulp and leaching of pulp inhibitors is probably lower than under natural conditions (Kelly et al. 2004). Burrows (1996) tested karaka germination success on filter paper in petri dishes and found zero germination in whole fruits. Burrows (1996) results indicated that karaka could be highly dependent on kereru to ingest fruits (Kelly et al. 2004). When tested in the field however, germination success was high for both whole karaka fruits and processed seeds (Robertson et al. 2006). Karaka seeds commence germinating some months after sowing, allowing time for insects and mammals to remove the fruit pulp prior to germination. These findings reinforce recent recommendations to conduct germination experiments in the field (Traveset & Verdú 2002; Kelly et al. 2004; Robertson et al. 2006).

Taraire fruit pulp removal at the start of the experiment increased not only germination success, but also seedling survival and growth (Table 5.5a), which may have been due to higher levels of seed predation (which continues post-germination) in whole fruits. Seedlings of large-seeded species such as taraire draw on seed reserves for many months after germination, and seed attack is probably detrimental to survival. Higher levels of pathogens and fungi can also occur in whole fruits (Traveset 1998), which may increase seedling mortality.

5.5.3 The role of introduced mammals

Separating the effects of introduced mammals and dispersal failure is difficult, as mammals can affect plant regeneration in numerous ways. Nevertheless, my results show that survival of both taraire and karaka was greater when mammals were excluded (Table 5.5; Figure 5.10). The effect was greater in karaka, where survival to both one and two years increased by up to two-fold when mammals were excluded (Figure 5.10). Even at Wenderholm, where pest control is intensive, introduced mammals decreased karaka survival by 28% after one year and 34% after two years. Taraire survival to one year decreased by 27% when mammals were not excluded.

Ship rats (*Rattus rattus*) and kiore (*Rattus exulans*) eat the pulp and destroy the seeds of many native New Zealand plants species (Beveridge 1964; Daniel 1973; Williams et al. 2000). Ship rats were probably responsible for the rodent seed predation at sites used in this study. Kiore are now largely absent from the New Zealand mainland, while ship rats are the most widespread rodent in low- and mid-altitude native forests (King 1995, pp. 178 & 213; Campbell & Atkinson 2002). On offshore islands, kiore depress karaka seedling recruitment compared to seedling establishment in rat-proof exclosures (Campbell & Atkinson 2002). Some seed predation in this study was probably also due to possums, which are known to eat the fruit pulp and destroy seeds of both karaka and taraire (Cowan 1990; Dijkgraaf 2002).

Karaka and taraire seed predation levels were extremely low compared to predation levels measured elsewhere (e.g. Wenny 2000). The proportion of cleaned karaka seeds removed or eaten by mammals (9% of uncaged seeds) was also lower compared to a site without mammal control (19% removal over a two-week period; Moles & Drake 1999). However, because mammal seed predation can occur over many months, Moles and Drake (1999) probably seriously underestimated the actual levels of seed predation, and hence the impact of predation on forest regeneration.

Kereru densities are lower in the presence of introduced mammals, because rats, possums, stoats, and cats prey on adults, chicks, and/or eggs (Clout et al. 1995b; Pierce & Graham 1995; Innes et al. 2004), and possums compete with kereru for food. Possums and rats also limit seed availability by destroying unripe and ripe fruits in the canopy prior to dispersal (Campbell & Atkinson 2002; Dijkgraaf 2002). When possum densities are high, almost all taraire fruits are destroyed before ripening (Dijkgraaf 2002, p. 180).

5.5.4 Reproductive dependence on seed dispersal

Karaka and taraire provide an interesting comparison of the potential risk (the combined likelihood and impact) of dispersal failure. Survival of dispersed (excluding the effects of caging) taraire seeds is around 3–4 times greater than undispersed seeds after one year. Taraire often fails to regenerate under its own canopy, and seedlings are rare compared to other canopy species (Dawson & Sneddon 1969). The thick, persistent litter layer that forms beneath taraire trees may inhibit regeneration of taraire seedlings, along with browsing by introduced mammals and destruction of seeds by pigs, possums, ship rats, and insects (Dawson & Sneddon 1969; Myers 1984; Dijkgraaf 2002). Because taraire has a much higher overall mortality rate than karaka, the contrast between dispersed and undispersed seeds is less striking. Taraire fruits are a preferred food in the diet of kereru (McEwen 1978), so probably have high dispersal rates when kereru are present.

Karaka is sometimes considered a weed in some areas of New Zealand where it has been introduced outside of its natural range and outcompetes other canopy species (Costall et al. 2006). Dense swards of karaka seedlings are often found beneath adult trees, particularly following exclusion of livestock. Nevertheless, survival of dispersed karaka seeds is up to 15 times higher than undispersed seeds at both one and two years. The high densities of karaka seedlings underneath conspecific adults are probably due to poor dispersal, as karaka is not a favoured food of kereru (Powlesland et al. 1997; Dijkgraaf 2002). Karaka was also dispersed historically through cultivation by humans (Costall et al. 2006), which may have enabled it to persist despite low palatability to frugivores combined with poor survival of undispersed seeds. Seeds may also be dispersed by gravity and in streams or other water sources, which may contribute to karaka regeneration. Because survival rates for dispersed karaka seeds are high, rare dispersal events may be sufficient for population maintenance or successful colonisation of new sites. Karaka are more vulnerable to mammal predation than taraire; thus, the combined benefits of seed dispersal and mammal exclusion increased taraire survival by more than seven-fold and karaka survival by four- to seventeen-fold.

In one of the few systems where the consequences of dispersal failure have been tested experimentally, Bond and Slingsby(1984) showed that inadequate dispersal increased post-dispersal seed predation of Proteaceous plants. The introduced Argentine ant (*Iridomyrmex humilis*) displaces native ant species in South African fynbos. In areas without native ants, Argentine ants are poor dispersers of native Proteaceae and seeds

suffer much higher levels of predation (Bond & Slingsby 1984). In addition, seed burial by native ants buffers Proteaceae populations from extinction after fire. Argentine ants fail to bury seeds, causing regeneration failure in Proteaceae after fire in areas without native ants (Christian 2001).

Some plant species may be buffered from extinction by traits including vegetative reproduction, persistent seed banks, or storage structures (Bond 1994). There is no evidence for persistent seed banks in either taraire or karaka, but karaka trees produce basal stem sprouts that appear to be capable of replacing the main stems of the parent tree if they die (Burrows 1994b).

5.5.5 Consequences of dispersal failure

To my knowledge, this is only the second study of dispersal failure to demonstrate experimentally that recruitment of undispersed seeds is lower than dispersed seeds, and the first was in a specialised ant-fire system (Christian 2001). Most studies have inferred a detrimental effect of dispersal failure on recruitment using observational methods, which are unable to distinguish between the effects of dispersal and other causes (e.g. Chapman & Chapman 1995; Cordeiro & Howe 2003; Traveset & Riera 2005). The consequences of seed dispersal disruption may not become evident for a long time, especially in long-lived tree species. Forests may contain adult trees that are unable to reproduce due to the loss of pollinators or seed dispersers — the so-called “living dead” (Janzen 1986). An example of this may occur on some Pacific Islands, where seed-dispersing pigeons are now extinct and fruit bats have declined substantially due to hunting, predation, and habitat loss (McConkey & Drake 2002). On islands where fruit bats still persist, the bats are ineffective dispersers at low population densities compared to high densities (McConkey & Drake 2002).

The disruption of seed dispersal mutualisms may have not only ecological, but also evolutionary consequences (Riera et al. 2002). Legitimate seed dispersers can exert selection pressure on plant populations, for example by selecting for particular traits such as fruit size or colour (Lord et al. 2002; Riera et al. 2002). Frugivore activity can also strongly influence the local genetic structure of plant populations (Shapcott 2000; Jordano & Godoy 2002). Metapopulation effects were not measured in this study, but may be extremely important for forest maintenance in a fragmented landscape. Dispersal failure and introduced mammals both have negative consequences for the regeneration of taraire

and karaka. The effects of kereru seed dispersal are unexpectedly large and persist for surprisingly long periods, beyond the dispersal and germination stages.

Chapter 6. Seed size variation, potential replacement dispersers, and effects on seedling size

Karaka (*Corynocarpus laevigatus*) fruits

6.1 Abstract

The New Zealand pigeon (kereru, *Hemiphaga novaeseelandiae*) is reported to be the sole remaining widespread disperser of large-seeded fruits. Many authors assume that the loss of kereru from native forests will have serious consequences for the regeneration of large-seeded trees. However, remaining animal species may replace kereru as seed dispersers if it becomes (locally) extinct. I asked the following questions: (1) Do large-seeded fruits vary sufficiently in diameter within a species for frugivores other than kereru to potentially disperse the smaller fruits? (2) Have frugivores other than kereru been recorded eating fruits of large-seeded species? (3) If only small fruits within a species are dispersed, will it affect seedling size?

Fruit diameter within a species varied considerably for three large-seeded species measured, within populations, between sites, and between years. Birds other than kereru have been observed feeding on fruits of nearly all large-seeded species. Birds routinely swallow fruits larger than their mean gape size, due to fruit handling methods,

discrepancies between measured gape width and actual bill capacity, and variation in gape width within a bird species.

A glasshouse experiment with tawa (*Beilschmiedia tawa*) showed that large seeds produced larger seedlings, with a similar mean effect size after both one and two years. Small-seeded tawa seedlings did not compensate for the initial disadvantage of small size with higher relative growth rates.

6.2 Introduction

The extinction of animal seed dispersers can have major consequences for plant populations and communities (Christian 2001). The extent to which dispersers are ecologically redundant will influence how great an effect their disappearance will have (Christian 2001; Loiselle & Blake 2002). If multiple dispersers are performing the same ecological role, then the loss of one disperser will probably not have a noticeable impact on plant populations (Loiselle & Blake 2002). However, where dispersal interactions are more specialised, other frugivores may be unable to provide effective dispersal services (Loiselle & Blake 2002). Dispersal of large-seeded species is more vulnerable to disruption than small seeds, as fewer animal species are large enough to disperse large seeds (Wheelwright 1985; Kitamura et al. 2002).

Following the extinction of a disperser, remaining or newly introduced species may shift their behaviour and act as ecological substitutes in seed dispersal (Loiselle & Blake 2002). For example, McConkey and Drake (2002) suggest that flying foxes have replaced an extinct pigeon in dispersing large seeds in Tonga. Introduced species can also act as seed dispersers in place of the lost native mutualists (Loiselle & Blake 2002), although they may not provide effective dispersal services (Bond & Slingsby 1984; Riera et al. 2002; Ness 2004).

Gape width tends to limit the size of fruits avian frugivores can swallow, particularly for single-seeded fruits (Wheelwright 1985). As a result, birds that act as replacement dispersers for large-seeded species may select smaller-than-average fruits. Larger seeds often have a higher probability of seedling survival and establishment under stressful conditions, both among (Leishman & Westoby 1994; Westoby et al. 1997; Moles & Westoby 2004) and within species (Howe & Richter 1982; Vaughton & Ramsey 1998; Paz & Martínez-Ramos 2003; Baraloto et al. 2005). However, seedlings from small seeds tend to have higher relative growth rates than large-seeded seedlings, especially when

resources are not limiting (Bloor & Grubb 2003; Baraloto et al. 2005). This trade-off between survival and growth rate could result in similar establishment probabilities for small and large seeds.

Following the arrival of humans in New Zealand, a number of bird species were driven to extinction (Holdaway et al. 2001). The New Zealand pigeon (kereru, *Hemiphaga novaeseelandiae*) is reported to be the sole remaining widespread disperser of five large-seeded plant species with fruits greater than 14 mm in diameter (Clout & Hay 1989). Kereru populations, however, are threatened by illegal hunting, habitat loss, and introduced predators (McEwen 1978; Clout et al. 1995a; Clout et al. 1995b). The (local) extinction of kereru could have serious consequences for large-seeded trees if seeds are not dispersed.

Other native and introduced birds may be able to act as dispersers if some fruits within a species are small enough for them to swallow. However, there are no published data on fruit size distributions for any of the large-seeded species, which are most vulnerable to dispersal failure. I asked the following questions: (1) Do large-seeded fruits vary sufficiently in size within a species for frugivores other than kereru to potentially disperse the smaller fruits? (2) Have frugivores other than kereru been recorded eating fruits of large-seeded species? (3) If only small fruits within a species are dispersed, will it affect seedling size (the best available measure of seedling fitness)?

6.3 Methods

6.3.1 Study sites and species

Clout & Hay (1989) reported that the fruits of karaka (*Corynocarpus laevigatus*), tawa (*Beilschmiedia tawa*), and taraire (*B. tarairi*) are all greater than 14 mm in diameter, and consequently kereru are the only bird capable of swallowing fruits of these species. Karaka is a canopy tree that grows up to 20 m tall and occurs as far south as Banks Peninsula in the South Island of New Zealand (Costall et al. 2006). Tawa grows up to 30 m tall and occurs throughout the North Island of New Zealand, where it is one of the main canopy tree species in lowland forests. Tawa is also found in the South Island, where it occurs to around 42° S (Knowles & Beveridge 1982). Taraire is a canopy tree that grows up to 20 m or more tall and is found in lowland and coastal forest from the north of the North Island to latitude 38° S (Allan 1961). Taraire and tawa fruits are important in the diet of kereru

(McEwen 1978), but karaka fruits are not favoured by kereru (Powlesland et al. 1997; DMW personal observation).

I collected karaka fruits from Otari-Wilton's Bush, Wellington (41° 15′ 57″ S, 174° 45′ 18″ E) in 2004 (n = 40) and 2005 (n = 92) and from Mt Tiger Bush, Whangarei (35° 45′ 04″ S, 174° 23′ 20″ E; n = 100) in 2005. Tawa fruits were collected from Otari-Wilton's Bush (n = 167) and Te Marua, Wellington (41° 06′ 34″ S, 175° 09′ 12″ E; n = 59) in 2004 and from Otari-Wilton's Bush (n = 100) and Blue Duck Reserve, Kaikoura (42° 14′ 10″ S, 173° 46′ 59″ E; n = 100) in 2005. I collected 100 taraire fruits from Ngunguru Rd, Whangarei (35° 40′ 08″ S, 174° 21′ 36″ E) in 2005. All sites were located in native forest within the distributional range of the species studied. For each species, I collected whole fruits directly from trees where possible, or else from the ground. Fruits were collected from and/or beneath an average of 13 trees and the diameter of fruits measured with digital callipers.

6.3.2 Tawa seedling size experiment

I conducted a seedling growth experiment in a glasshouse at the University of Canterbury, Christchurch using tawa seeds collected in Wellington in 2004. I weighed cleaned seeds to an accuracy of 0.01 g to obtain fresh weights and placed each seed in a separate labelled, sealed plastic bag until sowing. I sowed 225 tawa seeds individually in four 60-cell seed trays in seed sowing mix (containing $^1/_3$ peat, $^1/_3$ sand, $^1/_3$ fine bark, super phosphate, and dolomite lime). I placed seeds randomly both within cells and trays and labelled each cell with the seed number. Seeds were pressed lightly into the seed sowing mix, sprinkled with additional mix and covered with fine gravel to prevent predatory flies from laying eggs on the seeds. Trays were placed in the glasshouse where temperature was maintained above 5° C but otherwise unheated.

Measuring dry mass requires destructive sampling; I therefore estimated tawa seed initial dry mass using 20 seeds collected from Blue Duck Reserve, Kaikoura in 2005 and not used in the growth experiment. I weighed these seeds, dried them at 70° C for 72 hours in paper envelopes and reweighed them. I then returned the seeds to the oven for a further 24 hours and reweighed them to confirm they had dried to a constant weight. This relationship was used to estimate the dry weights of the seeds at the start of the experiment from their fresh weights.

At one year, I measured seedling height from the first leaf node to the stem tip. The first leaf node provides an easy and consistent guide to deciding where roots end and the

stem begins (Evans 1972). Measuring seedling height from the soil surface may accidentally allocate tissue from the stem to the root or vice versa, due to variation in seed depth at germination (Evans 1972). I also measured the length of the longest leaf, and counted the number of leaves for each seedling. To measure seedling biomass, I harvested tawa seedlings at one and two years after sowing. At one year, I harvested seedlings of the 25 lightest and 25 heaviest seeds and 50 randomly selected other seeds by cutting the stem at the first leaf node using secateurs. I placed the shoot (stem and leaves) of each harvested seedling in a separate, labelled paper bag and placed them in a drying oven within 2.5 hours of harvesting. After drying at 70° C for 48 hours I cooled seedlings in a desiccator in batches to prevent moisture absorption and weighed them. I returned seedlings to the drying oven for a further 24 hours at 70° C, and then reweighed ten seedlings to confirm that they had dried to a constant weight.

I transplanted all remaining seedlings (n = 100) into larger individual pots with potting mix containing 9-month slow-release fertiliser. At two years (one year after repotting), I harvested both the shoots and roots of a further 70 seedlings. Although there was no mortality between one and two years, some seedlings had brown leaves and so were not harvested. I cut seedling stems at the first leaf node and placed the shoot of each seedling into a separate, labelled paper bag. I repeated the drying and weighing process carried out at one year (described above), placing shoots in a drying oven within 2.5 hours of harvesting. I then gently separated seedling roots from the potting mix, rinsed them under tap water to remove any remaining particles, and placed the roots of each seedling into a separate, labelled paper bag. Seeds had disintegrated by this stage. Roots were placed in a drying oven within five hours of harvesting.

6.3.3 Statistical analysis

I analysed the relationship between tawa fresh and dry seed mass using linear regression. I then estimated the dry mass of seeds used in the growth experiment using this regression equation. I analysed the effect of estimated initial seed dry mass on germination success, and survival of germinated seeds to one year, using binomial generalised linear models. For all tawa seedlings surviving at one year, I used linear regression to analyse the relationship between estimated initial seed dry mass and (1) the number of leaves (log transformed), (2) longest leaf length, and (3) seedling height. For tawa seedlings harvested at one year, I also analysed the relationship between estimated initial seed dry mass and final above ground (shoot) dry mass, using linear regression. For two year old seedlings, I

used linear regression to analyse the relationship between estimated initial seed dry mass and (1) shoot dry mass, (2) root dry mass, and (3) total seedling dry mass. I also analysed the relationship between estimated seed dry mass and relative growth rate in tawa seedlings after two years using linear regression. Relative growth rate (RGR) was calculated using the equation:

$$\text{RGR} = \frac{\log(\text{final seedling dry mass (g)}) - \log(\text{seed dry mass (g)})}{\text{number of days after sowing}}$$

which gives seedling growth rate (in g g^{-1} day^{-1}) over the two year period of the experiment. I carried out all analyses using R version 2.4.1 (R Development Core Team 2006).

6.4 Results

6.4.1 Fruit size variation

Mean fruit diameter across sites and years ranged from 16.8 mm (± 1.6 SD) for tawa, to 19.1 mm (± 2.4) for karaka, and 19.4 mm (± 1.3) for taraire. Fruit diameter varied considerably within populations for all three species, and between years and sites for karaka and tawa (Figure 6.1). Tawa fruits collected from two sites in Wellington (Otari-Wilton's Bush and Te Marua) in 2004 did not differ significantly in fruit diameter, and are shown combined in Figure 6.1 (two-sample t-test, t = –0.41, d.f. = 224, P = 0.68). Karaka fruits were the most variable, ranging in diameter from 12.0–31.1 mm.

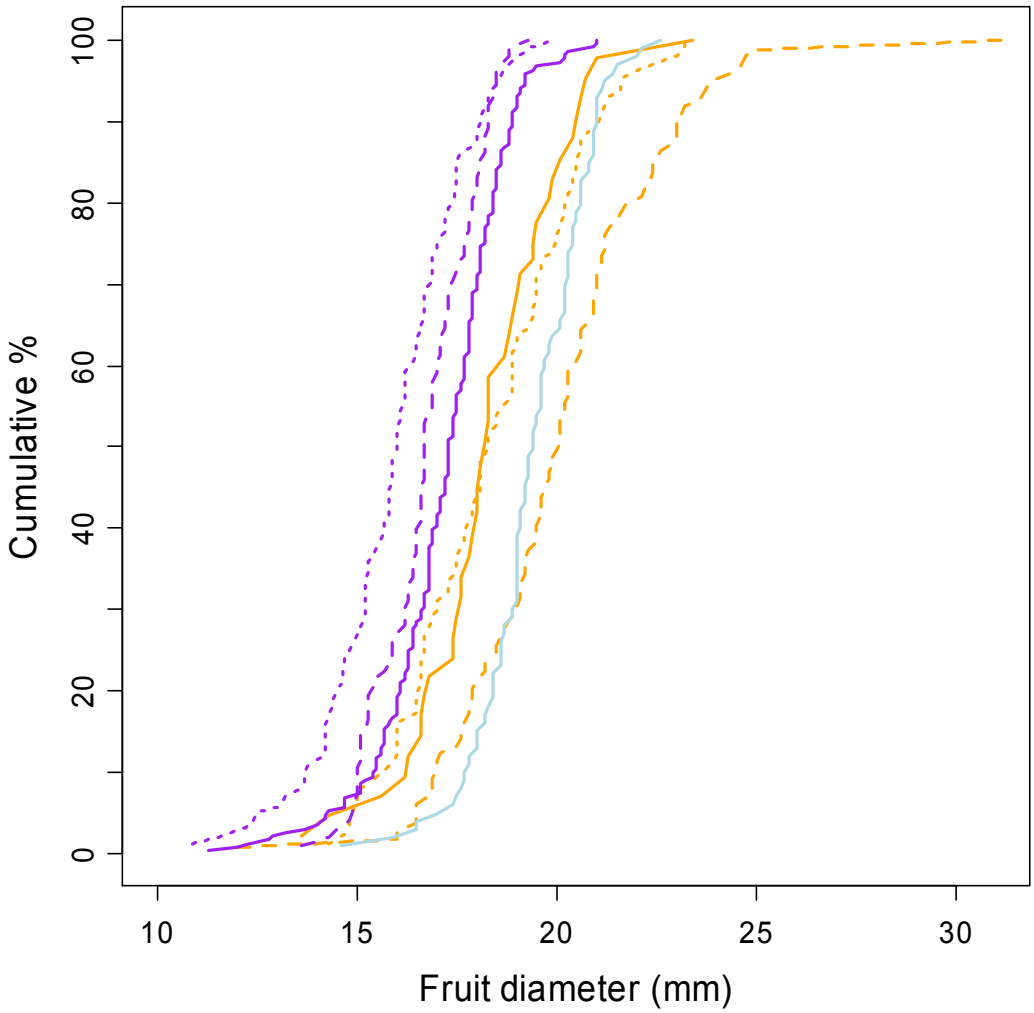

Figure 6.1 Variation in fruit diameter among sites and years for the large-seeded trees karaka (*Corynocarpus laevigatus*), tawa (*Beilschmiedia tawa*), and taraire (*B. tarairi*). Karaka fruits are shown in orange (Wellington 2004 = solid line, Wellington 2005 = dotted line, Whangarei 2005 = dashed line). Tawa fruits are shown in purple (Wellington 2004 = solid line, Wellington 2005 = dotted line, Kaikoura 2005 = dashed line). Taraire fruits are shown in light blue.

6.4.2 Potential replacement dispersers

Based on bird gape sizes of museum specimens reported by Clout & Hay (1989), none of the fruits measured were small enough to be swallowed by birds other than kereru. However, Anderson (1997, and personal communication) measured gape sizes in live birds for tui (n = 2), blackbirds (n = 9), saddlebacks (n = 14), stitchbirds (n = 3), bellbirds (n = 22), and silvereyes (n = 22). For some species, gapes sizes were larger in Anderson (1997) compared to those reported by Clout & Hay (1989; Table 6.1). Anderson (1997) also reported the mean and standard error about the mean, and the maximum in her samples (Table 6.1). Based on Anderson's (1997) data, the 95th percentile for bellbird gape width is 8.2 mm, which corresponds well with the maximum observed (8.5 mm). For tui there are few data, but the larger of the two measured was 11.0 mm, and from this small sample the 95th percentile would be around 12.7 mm, which might allow the largest tui to swallow fruits up to 14 mm in diameter. For karaka, 0–2.5% of fruits from Wellington (in 2004 and 2005 respectively) and 1% of fruits from Whangarei were 14 mm or less in diameter. A greater proportion of tawa fruits were less than or equal to 14 mm in diameter (3.5% and 11% of Wellington fruits in 2004 and 2005 respectively, and 1% of Kaikoura fruits). No taraire fruits collected were 14 mm or less in diameter.

There are isolated reports of native birds other than kereru eating fruits of all species with fruits greater than 14 mm in diameter, except for tawapou (*Planchonella costata*; Table 6.1), which is rare. Tui have been reported eating fruits of most of the large-seeded tree species (Table 6.1), including one observation of a flock of around 12 individuals feeding on tawa fruits (Booth 1984). Kokako eat tawa and taraire fruits and stitchbirds have been reported eating fruits of karaka, although both of these birds are extremely rare (Table 6.1). Higgins et al. (2001) also listed stitchbirds feeding on karaka fruits, but I was unable to find this in their cited reference (Gravatt 1969), and have therefore not included it in Table 6.1. There are no known published records of introduced birds eating fruits in the category > 14 mm in diameter (Table 6.1).

All reports of birds feeding on large-seeded fruits were from feeding observations, rather than defecation of seeds, and fruit handling methods were usually not reported. Dijkgraaf (2002) did distinguish fruit swallowing from pulp theft, noting that silvereyes pecked karaka fruit pulp rather than swallowing fruits whole (not included in Table 6.1). Dijkgraaf (2002) observed tui swallowing puriri fruits on three occasions (11% of tui frugivory observations), and myna on one occasion (10% of myna frugivory observations).

However, birds foraging in the canopy are often difficult to observe, and for some of the records in Table 6.1 it is possible that the birds were feeding on insects or flowers, or pecking at fruit pulp.

Table 6.1 Bird species† recorded feeding on fruits of large-seeded plant species in New Zealand. Adapted from Clout & Hay (1989 = a) with additional bird feeding observations collated by Jenny Ladley and DMW (b = Oliver 1955, p. 503; c = Gibb 1970; d = Falla et al. 1978, p. 204; e = Stewart 1980, p. 26; f = Booth 1984; g = Myers 1984, p. 55; h = Flux 1994; i = O'Donnell & Dilks 1994; j = Anderson 1997, p. 87; k = Higgins et al. 2001, p. 957; l = Dijkgraaf 2002, p. 145; m = Williams 2003). A blank indicates no data.

Fruit diameter[1]	Plant species	Common name	Myna*	Silvereye	Bellbird	Stitchbird	Saddleback	Starling*	Blackbird*	Tui	Thrush*	Kokako	Weka	Kereru	Brown kiwi
>14 mm	*Corynocarpus laevigatus*	karaka								b,d,e				a	
	Vitex lucens	puriri	l							e,l				a	
	Beilschmiedia tarairi	taraire										g		a	
	B. tawa	tawa								f		f,h		a	
	Planchonella costata	tawapou												a	
>10 mm	*Prumnopitys ferruginea*	miro			i				a	a		a	a	a	a
	Syzygium maire	swamp maire										a		a	
	Dysoxylum spectabile	kohekohe		j		j,k	j			e,j		a	a	a	
	Litsea calicaris	mangeao										a		a	
	Elaeocarpus dentatus	hinau										a	a	a	a
	Ripogonum scandens	supplejack		i	i	k			a	a	a	a		a	
	Clout & Hay (1989)			5	6	7	8	9	9	9	10	13	13	14	24
Gape size (mm)	Anderson (1997) and	mean		5.1	6.5	7.6	7.1		10.7	10.8	11.8				
	Anderson pers. comm.	SD		0.37	1.03		1.32		1.26						
		n		22	22	3	14		9	2	1				
		maximum		6.3	8.5	8.6	9.0		13.0	11.0					
Largest fruit diameter (mm) reported swallowing				9.9[m]	9.7[m]					14‡				25[c]	

† For full bird names see Heather and Robertson (2000); * indicates introduced species; ‡ extrapolated from minimum karaka fruit diameter.

6.4.3 Effect of seed size on seedling size

Fresh mass for seeds used in the tawa growth experiment varied more than seven-fold, ranging from 0.5–3.8 g (Figure 6.2a). There was a strong correlation between wet seed mass and dry seed mass in tawa ($R^2 = 0.92$, F = 218.48, d.f. = 18 and 1, P < 0.0001), described by the linear regression equation:

Seed dry mass (g) = 0.43 x seed wet mass (g) – 0.0074

Seed mass had no effect on germination success (d.f. = 1 and 223, deviance = 69.1, residual d.f. = 223, residual deviance = 68.44, Z = 0.81, P = 0.42), with 96% of all seeds sown germinating. Seed mass also had no effect on survival to one year (d.f. = 1 and 215, deviance = 114.22, residual d.f. = 215, residual deviance = 114.1, Z = 0.35, P = 0.72), with 93% of germinated seeds surviving. Tawa seedlings were still attached to the seed at one year, which appeared to be relatively intact (Figure 6.2b).

(a) (b)

Figure 6.2 (a) Tawa (*Beilschmiedia tawa*) seeds varied considerably in size, with seeds used in the seedling growth experiment ranging in wet mass from 0.5–3.8 g (Photo: Matt Walters); (b) Tawa (*Beilschmiedia tawa*) seedling harvested one year after sowing. The relatively intact seed is still attached to the seedling.

After one year, smaller tawa seeds had produced smaller seedlings than larger seeds with estimated seed dry mass positively correlated with all measures of seedling size (Figure 6.3). Seed mass explained 29% of the variance in leaf number ($R^2 = 0.29$, $F = 84.33$, d.f. = 1 and 199, $P < 0.0001$; regression equation = 1.7191 + 0.69634 x) and 33% of the variance in longest leaf length ($R^2 = 0.33$, $F = 100$, d.f. = 1 and 199, $P < 0.0001$; regression equation = 49.266 + 24.548 x). Seed mass was more strongly related to seedling height than leaf number or length, explaining 48% of the variance ($R^2 = 0.48$, $F = 187.2$, d.f. = 1 and 199, $P < 0.0001$; regression equation = 19.283 + 64.209 x). Estimated seed dry mass was most strongly correlated with shoot biomass, explaining 58% of the variance in seedling above ground biomass at one year ($R^2 = 0.58$, $F = 138.3$, d.f. = 1 and 98, $P < 0.0001$; regression equation = 0.02338 + 0.41381 x).

Although the relationship between seed mass and seedling size was still significant after two years, there was much more variation among individual seedlings (Figure 6.4). After two years, estimated seed dry mass explained only 18% of the variance in both shoot dry mass ($R^2 = 0.18$, F = 16.44, d.f. = 1 and 68, P = 0.0001; regression equation = 2.4054 x – 0.2758) and root dry mass ($R^2 = 0.18$, F = 15.83, d.f. = 1 and 68, P = 0.0002), and 19% of the variance in total seedling dry mass ($R^2 = 0.19$, F = 17.51, d.f. = 1 and 68, P < 0.0001; regression equation = 3.3779869 x – 0.0009248).

The effect of seed mass on seedling biomass at two years was dominated by five large seeds that produced large seedlings (Figure 6.4). When these five seedlings were removed from the total biomass analysis, the effect was still significant but the amount of variance explained was much smaller ($R^2 = 0.08$, F = 5.251, d.f. = 1 and 63, P = 0.025). Seedlings harvested at one year had a much wider seed mass range than those harvested at two years (because the seedlings from the smallest and largest seeds were harvested at one year). When the relationship between seed dry mass and shoot dry mass at one year was reanalysed using only those seeds in the size range of seeds harvested at two years, the amount of variance explained was reduced by 50% ($R^2 = 0.29$, F = 21.23, d.f. = 1 and 49, P < 0.0001).

Using the regression equations for the relationship between seed dry mass and shoot dry mass, an 8-fold increase in seed mass (from 0.75 to 1.35 g) confers a seedling size advantage of 1.7-fold at one year and 1.9-fold at two years. Hence, there was no evidence that the mean effect of seed size on seedling size had become weaker with a longer growth interval, even though the variance had increased. There was no relationship between estimated seed dry mass and relative growth rate in tawa seedlings over the two year period of the experiment ($R^2 < 0.001$, F = 4.1, d.f. = 1 and 68, P = 0.995; Figure 6.4).

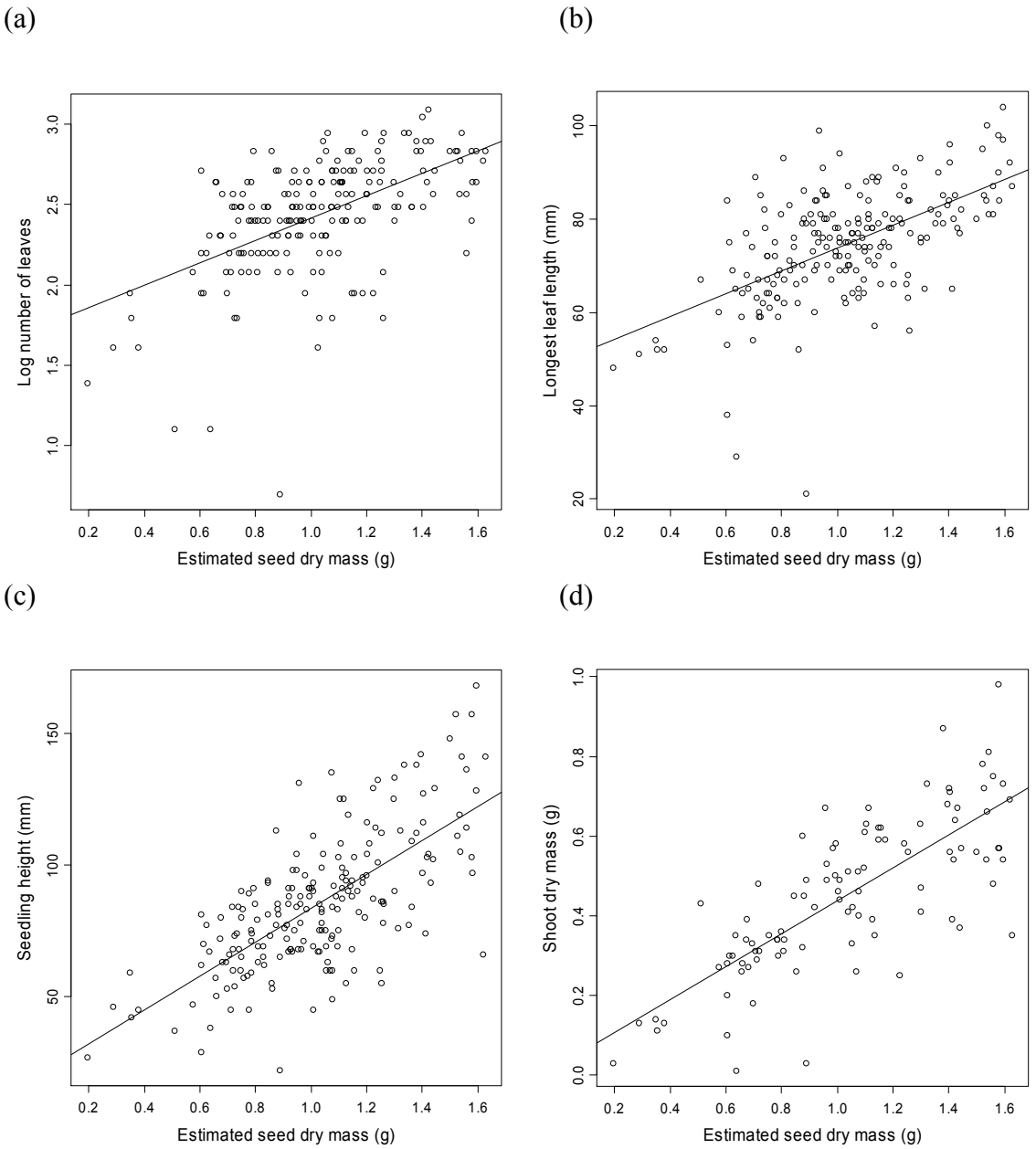

Figure 6.3 Relationship between seed dry mass and seedling size in tawa (*Beilschmiedia tawa*) seedlings at one year. (a) number of leaves ($R^2 = 0.29$, $P < 0.0001$); (b) length of longest leaf ($R^2 = 0.33$, $P < 0.0001$); (c) seedling height ($R^2 = 0.48$, $P < 0.0001$); (d) above ground dry mass ($R^2 = 0.58$, $P < 0.0001$). I estimated seed dry mass from seed wet mass using a regression equation derived from 20 tawa fruits with known wet and dry weights.

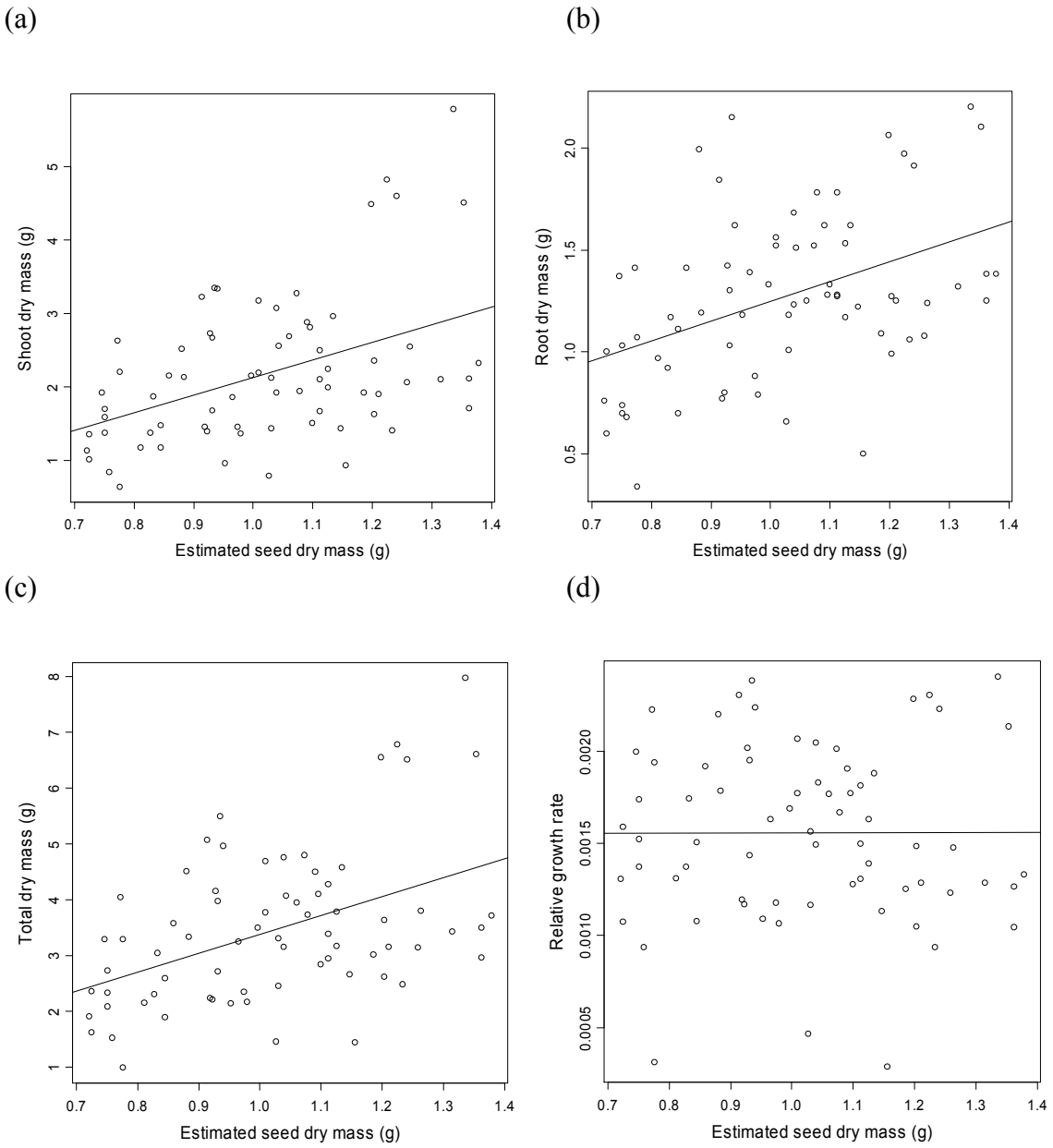

Figure 6.4 Relationship between seed dry mass and seedling size and growth rates in tawa (*Beilschmiedia tawa*) seedlings at two years. (a) above ground (shoot) dry mass ($R^2 = 0.18$, $P = 0.0001$); (b) root dry mass ($R^2 = 0.18$, $P = 0.0002$); (c) total seedling dry mass ($R^2 = 0.19$, $P < 0.0001$); (d) relative growth rate (g g^{-1} day^{-1}; $R^2 < 0.0001$, $P = 0.995$). I estimated seed dry mass from seed wet mass using a regression equation derived from 20 tawa fruits with known wet and dry weights.

6.5 Discussion

6.5.1 Seed size variation and potential replacement dispersers

Large-seeded fruits varied considerably in size and in most species fewer than 5% of fruits were 14 mm or less in diameter, which tui could potentially swallow. Birds other than kereru have been observed occasionally eating fruits of karaka, tawa, taraire, and other large-seeded species (Table 6.1). Although gape width generally limits the size of fruits that can be swallowed (Wheelwright 1985), some birds avoid gape-limitation by squashing fruits in the bill before swallowing them (Levey 1987). Silvereyes have even been observed whacking mistletoe fruits against branches to force them down their throats (Ladley & Kelly 1996). Measured gape widths are only a rough estimate of bill capacity (Clout & Hay 1989), and gape width also differs among individual birds within a species (Anderson 1997).

Kereru are an extreme example of gape limitation avoidance, for although their gape width is 14 mm, the distensible gape enables them to swallow fruits up to 25 mm in diameter (Gibb 1970). Clout & Hay (1989) reported that blackbirds, tui, and thrushes disperse fruits between 10–14 mm diameter, even though these birds have measured gapes of 9–10 mm. Multiple authors have reported tui feeding on karaka fruits (Oliver 1955; Falla et al. 1978; Stewart 1980), which average around 19 mm in diameter, though tui might be expected to take mainly the smallest fruit. Silvereyes dispersed seeds from several species with a mean fruit diameter of nearly 10 mm, almost twice their mean gape width of 5 mm, and bellbirds (with a mean 6–7 mm gape width) also swallowed fruits of this size (Williams & Karl 1996). Anderson's (personal communication) work shows that part of this may be due to larger individual birds, which often have gape sizes 25-30% larger than the mean.

While seed size within a plant species generally decreases with increasing latitude (Moles & Westoby 2003), bird mass (and presumably gape width) increases (Ashton 2002). However, as most of the species with the largest fruits are restricted to northern New Zealand (Allan 1961), any additional overlap in the upper gape limit of alternative dispersers and the lower limit in fruit diameter may be limited. Species with medium-seized fruits (10–14 mm diameter) such as miro (*Prumnopitys ferruginea*), hinau (*Elaeocarpus dentatus*), and supplejack (*Ripogonum scandens*) are found further south, where a wider range of potential dispersers may be available.

Although species such as tui may disperse large-seeded tree species only occasionally, rare dispersal events can have a disproportionate effect (Clark et al. 1998b). For example, carnivorous mammals removed only around 15% of *Prunus mahaleb* fruits, but were responsible for 67% of long-distance dispersal events (Jordano et al. 2007). Nevertheless, frugivores may avoid trees where they are able to swallow only a small proportion of available fruits.

Based on published feeding observations, introduced birds do not appear to be potential replacement dispersers for the largest of the large-seeded species. Although blackbirds and thrushes eat medium-sized fruits such as supplejack and miro, introduced birds do not eat large quantities of fruits from native plants (Kelly et al. 2006). In a review of avian fruit-visitors to native plants in New Zealand, introduced birds contributed on average 5% to fruit visits (Kelly et al. 2006). Blackbirds were the most important introduced bird contributing 3.9% to all fruit visits, but contributions by the rare saddleback were nearly as high, even though it was present at only one of the ten study sites (Kelly et al. 2006).

Introduced mammals may have the potential to act as replacement seed dispersers in New Zealand, although small mammals are unlikely to disperse large-seeded species. Mice and kiore generally destroy all seeds eaten, while ship rats disperse only some small-seeded species (Williams et al. 2000). Possums act as both seed dispersers and seed predators, but apparently do not swallow fruits > 10 mm in diameter (Cowan 1990; Williams et al. 2000; Dungan et al. 2002). Pigs are primarily seed predators, destroying seeds of taraire (Dawson & Sneddon 1969), hinau, matai (*Prumnopitys taxifolia*), and miro (Beveridge 1964), but can disperse some seeds intact (Beveridge 1964; Williams 2003). Knowles & Beveridge (1982) reported that pigs eat large quantities of tawa fruits, but did not comment on whether any of the seeds were intact. The potential for other large-bodied introduced mammals including goats and deer to disperse seeds is unknown. Quantitative studies are required to ascertain whether any birds and introduced mammals are important alternative dispersers of large-seeded trees in New Zealand.

6.5.2 Effects of seed size on seedling size

Dispersal of only small seeds by replacement frugivores may be detrimental to seedling growth, and consequently seedling fitness. In tawa, smaller seeds produced smaller seedlings when grown in a glasshouse, even after two years. The mean effect of seed size on seedling size was comparable at both one and two years. Importantly however, even in

the glasshouse the variance explained by seed size decreased over time, as other factors affecting seedling growth accumulated (taking above-ground dry mass and a similar range of predictor sizes, the R^2 went down from 0.29 to 0.18 from the first year to the second). Howe and Richter (1982) found a strong effect of seed mass on *Virola surinamensis* seedling size after 15 weeks when seedlings were grown in the glasshouse. *V. surinamensis* seedlings also appeared to do better with a small-seeded conspecific competitor than a large-seeded one (Howe & Richter 1982). For seven species of *Psychotria* tested in the field, seed mass had a positive effect on seedling biomass in five species and on survival in six species after one year (Paz & Martínez-Ramos 2003).

Tawa seedlings from small seeds did not compensate for the initial size disadvantages of small seed mass by having a higher relative growth rate than large-seeded seedlings. Higher relative growth rates in small-seeded seedlings appear to be common, both within (Paz & Martínez-Ramos 2003; Baraloto et al. 2005) and among species (Bloor & Grubb 2003).

Under natural conditions, environmental factors that are absent in the relatively benign conditions in a glasshouse could have a significant effect on seedling mortality. Larger seeds can have an establishment advantage under a range of environmental stressors, including shade (Leishman & Westoby 1994), herbivory or seedling damage (Green & Juniper 2004), and deep litter (Molofsky & Augspurger 1992). Greater seed resources can increase the ability of seedlings to support metabolic carbon demands in low light levels or to resprout after damage (Green & Juniper 2004). Paz and Martínez-Ramos (2003) found that positive effects of seed mass on survival and growth were stronger under natural conditions than in a glasshouse, where they were mostly restricted to seedlings at low light levels. However, environmental disturbance such as heavy rainfall events and branch- or tree-fall could significantly affect survival and are probably independent of seed or seedling size. Hence, in the field smaller seedlings may sometimes outlive larger conspecifics by chance alone. To confirm the effect of seed mass on seedling size in tawa, experiments should be conducted in the field. Field experiments will also clarify whether larger seedling size confers a survival advantage under natural conditions, where environmental stochasticity may override any benefits of large size.

Chapter 7. Fruit size preference in the New Zealand pigeon (*Hemiphaga novaeseelandiae*)[2]

Kereru have a distensible gape, enabling them to swallow large fruits such as tawa (Photo: Matt Walters).

7.1 Abstract

We investigated whether the New Zealand pigeon *Hemiphaga novaeseelandiae* (Columbidae) exhibits size-based preferences for fruits. We tested the hypothesis that in small-fruited species, pigeons would prefer larger fruits, but in larger-fruited species, this preference would reverse as the pigeons become increasingly limited by their gape size. We collected undispersed fruits and bird-dispersed seeds of ten plant species, some over several sites or years (13 datasets in total). We estimated the fruit size of dispersed seeds by fitting regressions of fruit diameter to seed diameter in intact fruits. We were able to predict fruit diameter from seed diameter in 12 of the 13 populations, although the relationship was stronger in single-seeded species than in multi-seeded species. Seven of the twelve populations tested showed a significant difference in seed diameter among undispersed and dispersed seeds. However, our results showed no consistent pattern in fruit

[2] This chapter has been accepted for publication (Wotton & Ladley in press). Contributions: JJL & DMW collected data; DMW & JJL analysed data; DMW wrote manuscript.

size preference by the New Zealand pigeon and did not support our hypothesis. The large-bodied New Zealand pigeon is generally not gape-limited and fruit size preferences appear to be independent of mean fruit size.

7.2 Introduction

Variation in fruit size has important implications for the evolution of fruit-eating animals and the plants they disperse. In order for dispersers to influence the evolution of fruit traits, frugivores must be able to discriminate between and have preferences for particular fruit characteristics. If frugivores showed size-based preferences, there could be important consequences for plant fitness and evolution. Non-random removal of fruits by animal frugivores can affect plant fitness if it changes the probability of recruitment. This in turn may influence the evolution of fruit traits where some of the variation in that trait is heritable (Wheelwright 1993).

A number of factors influence fruit choice in fruit-eating animals, including fruit colour, fecundity, and fruit size. Although these traits vary considerably among different plant species, there can also be substantial variation within a species. Fruit size is a prime candidate for coevolution between plants and their dispersers, as it is correlated with disperser type (Jordano 1995a), can be highly variable within a species (Michaels et al. 1988), and is heritable in at least some species (Wheelwright 1993; Cheng et al. 2004). Recent research also indicates an association between evolutionary divergences in seed mass and divergences in seed dispersal syndrome (Moles et al. 2005).

Fruit or seed size can differ among years, among populations, among plants within a population, and among fruits within an individual plant (Howe & Vande Kerckhove 1981; Jordano 1984; Michaels et al. 1988; Obeso 1993; Wheelwright 1993; Jordano 1995b; Parciak 2002). Although this variation in fruit size may shape the interaction between frugivores and their food plants, selection forces may be acting in opposing directions. Fruit size is generally closely correlated with seed size (Wheelwright 1993; Alcantara & Rey 2003), and both large and small seeds have differing advantages. Although large fruits provide a greater reward, frugivores can be limited by their gape width in the maximum size of fruits they can swallow (Wheelwright 1985; Jordano 1987). This is particularly true for single-seeded fruits, which usually have to be swallowed whole to be dispersed. In multi-seeded species, frugivores may avoid gape limitation by biting off pieces of the fruit or mashing fruits prior to swallowing (Levey 1987). Fleshy-fruited

plants with smaller seeds therefore tend to have more species of potential dispersers (Wheelwright 1985; Kitamura et al. 2002), and smaller seeds may be more likely to be dispersed (Howe & Vande Kerckhove 1981). Larger seeds are beneficial during seedling establishment under a wide range of conditions (Howe & Richter 1982; Howe et al. 1985; Leishman & Westoby 1994; Westoby et al. 1997; Moles & Westoby 2004). Therefore selection in either direction could have important consequences for plant recruitment.

Both physical limits to fruit handling or ingestion (including gape limitation), and profitability may influence fruit size selection by frugivores. Foraging animals use decision cues such as fruit size as an indicator for the most profitable food item (Barnard & Brown 1981). Fruit size preference by birds within a plant species has been measured in only a few studies (Howe & Vande Kerckhove 1981; Sallabanks 1993; Wheelwright 1993; Parciak 2002; Alcantara & Rey 2003). These studies all measured fruit size preference for a single plant species, and results among them are inconsistent. For multi-seeded species, a lack of fruit size preferences in at least some frugivore species may be accounted for by fruit handling techniques that enable gape limitation avoidance (Levey 1987). For species with single-seeded fruits, we predict that birds are likely to consume larger-than-average fruits when (1) fruits are small relative to the size of the bird and gape size is not a limiting factor; and (2) when all fruits are equally accessible, or large fruits are more accessible, or the reward for larger fruits outweighs the cost to frugivores in searching for them. In contrast, birds are likely to consume smaller-than-average fruits when (1) fruits are large in comparison to the size of the bird so gape size limits consumption of larger fruits; or (2) small fruits are more accessible or palatable than large fruits. The aim of this study was to investigate whether there is a consistent pattern in fruit size selection by a single avian seed disperser across several plant species.

In this paper we tested whether an important New Zealand frugivore, the New Zealand pigeon (*Hemiphaga novaeseelandiae*, Columbidae) selects fruits non-randomly by size from the fruits on offer. The New Zealand pigeon is virtually the sole disperser of fruits greater than 10 mm in diameter in New Zealand (Clout & Hay 1989). Other frugivores that previously dispersed large-fruited species in New Zealand are either extinct or so restricted in distribution that they no longer provide effective dispersal (Clout & Hay 1989). New Zealand pigeons consume fruits of at least 70 different plant species (Clout & Hay 1989), across a wide range of fruit sizes. The gape width of the New Zealand pigeon is 14 mm (Clout & Hay 1989), although its distensible gape enables it to swallow fruits up to 25 mm diameter (Gibb 1970). There are no precise data on fruit size distributions for

large fruited species in New Zealand. Therefore, we do not know how many species have fruits of a diameter above the pigeon's gape limit. If some fruits are larger than the swallowing capacity of the pigeon, gape limitation will occur. We tested the hypothesis that in small-fruited species pigeons will prefer larger-than-average fruits, but in large-fruited species this preference will reverse as the pigeons become increasingly gape-limited.

7.3 Methods

7.3.1 Study sites and species

The New Zealand pigeon is a large (c. 650 g) pigeon (Clout et al. 1995b) that eats only fruits, flowers, and (when fruit is scarce) leaves (McEwen 1978). New Zealand pigeons swallow fruits whole and defecate the seeds intact. Although regurgitation is common for many avian frugivores (Levey 1986), this has been reported only on a single occasion for the New Zealand pigeon (McEwen 1978). Although the pigeon is widespread throughout New Zealand and relatively common, it is threatened by habitat loss, predation by introduced mammalian pests, and illegal hunting (McEwen 1978; Clout et al. 1995a; Clout et al. 1995b).

This study was carried out at eight sites from around New Zealand within the distributional range of the plant species studied (Table 7.1). All sites were located in native forest. We collected data for ten plant species known to be consumed by the New Zealand pigeon (McEwen 1978). Prior to our study, it was unknown which of the study species had fruits greater in diameter than the swallowing limit of pigeons (25 mm). We included four species with a fruit diameter greater than 14 mm (the limit above which the New Zealand pigeon is the only known disperser; Clout & Hay 1989), three species with a diameter between 10 mm and 14 mm (for which the New Zealand pigeon is the only widespread disperser; Clout & Hay 1989), and three species less than 10 mm in fruit diameter.

For each species, we collected 100 fallen intact fruits (hereafter referred to as "undispersed") from beneath an average of eleven trees. At the same time we collected between 41 and 100 dispersed seeds of the same species. Bird dispersed seeds were easily recognisable, with the fruit pulp cleanly removed, and seeds often deposited beneath perches. Each species was collected at one or two sites and for one to three years (Tables

7.1 and 7.2). The length and width of fruits and seeds were measured with digital callipers and the number of seeds within each fruit was also recorded.

Although we generally did not see birds defecating the dispersed seeds, we are confident that the New Zealand pigeon was the primary frugivore for the dispersed seeds we collected for this study. The majority of the species studied were too large for other frugivores to swallow (Clout & Hay 1989). In addition, we made direct observations of the New Zealand pigeon feeding on fruits and defecating seeds of the study species at a number of the sites at the time of collection. At many of the sites, the Zealand pigeon was the most abundant or the only frugivorous bird observed. For the three species with a fruit diameter less than 10 mm (pigeonwood (*Hedycarya arborea*), ngaio (*Myoporum laetum*), and nikau (*Rhopalostylis sapida*)) there was a range of potential dispersers in addition to pigeons. However, pigeonwood seeds at Kaikoura were collected from large piles of seeds typically found beneath pigeon roosts. Pigeons were the only birds we observed feeding on pigeonwood fruits at the Northland site, and also on nikau fruits in trees beneath which we collected seeds in Canterbury. We observed pigeons feeding on ngaio fruits in Akaroa on other occasions, but fruits may also have been eaten by native bellbirds (*Anthornis melanura*) and silvereyes (*Zosterops lateralis*), or introduced starlings (*Sturnus vulgaris*) and blackbirds (*Turdus merula*). Kohekohe (*Dysoxylum spectabile*) and supplejack (*Ripogonum scandens*) fruits may have been eaten by both tui (*Prosthemadera novaeseelandiae*) and pigeons, although pigeons are most commonly observed feeding on these fruits.

Table 7.1 The plant species and sites for which undispersed and bird-dispersed fruits and seeds were collected. Latitude and longitude are given as degrees, minutes, and seconds.

Plant species	Common name	Region	Site	Latitude (S)	Longitude (E)	Elevation (m)
Corynocarpus laevigatus	karaka	Northland	Mt Tiger Rd	35° 45′ 04″	174° 23′ 20″	180
Dysoxylum spectabile	kohekohe	Northland	Whale Bay	35° 33′ 29″	174° 30′ 04″	40
Myoporum laetum	ngaio	Canterbury	Akaroa	43° 48′ 11″	172° 58′ 16″	40
Rhopalostylis sapida	nikau	Canterbury	Nikau Palm Gully	43° 52′ 01″	172° 57′ 36″	160
Hedycarya arborea	pigeonwood	Kaikoura	Blue Duck Reserve	42° 14′ 10″	173° 46′ 59″	420
Hedycarya arborea	pigeonwood	Northland	Mt Tiger Rd	35° 45′ 04″	174° 23′ 20″	180
Ripogonum scandens	supplejack	Kaikoura	Blue Duck Reserve	42 ° 14′ 10″	173° 46′ 59″	420
Syzygium maire	swamp maire	Kapiti	Nga Manu Reserve	40° 51′ 47″	175° 03′ 36″	10
Beilschmiedia tarairi	taraire	Northland	Ngunguru Rd	35° 40′ 08″	174° 21′ 36″	115
Beilschmiedia tawa	tawa	Kaikoura	Blue Duck Reserve	42° 14′ 10″	173° 46′ 59″	420
Planchonella costata	tawapou	Northland	Whale Bay	35° 33′ 29″	174° 30′ 04″	40

7.3.2 Statistics

For dispersed seeds we knew only the seed size, not the fruit size before ingestion. Therefore, we first analysed within species the relationship between seed diameter and fruit diameter for undispersed seeds using linear regression, to establish whether seed size could be used to predict fruit size. Next, we used ANOVA to determine within species whether mean seed diameter differed among dispersed and undispersed seeds for each species at each site and year of collection.

Finally, we analysed the effect of mean fruit diameter across plant species on fruit size preference within species using linear regression. Fruit size preference was calculated for each species as the mean diameter of undispersed fruits minus the mean estimated diameter of dispersed fruits (calculated using regression equations derived above, Table 7.2). All data were analysed using R version 2.1.1 (R Development Core Team 2005).

7.4 Results

Mean fruit diameter ranged from 8.0–20.1 mm (Table 7.3). Only one species (karaka, *Corynocarpus laevigatus*) had fruits larger than 25 mm diameter (Table 7.4). Seed diameter in single-seeded species explained between 42–82% of the variance in fruit diameter (Table 7.2). We used the seed diameter of dispersed seeds to predict the size of fruits that were consumed for single-seeded species.

The correlation was much weaker for multi-seeded species. Although P-values were statistically significant for two of the three multi-seeded species, seed diameter explained only 24–25% of the variance in fruit diameter in these two species (Table 7.2). For multi-seeded species we searched for a better alternative predictor of fruit diameter. There was a significant and positive correlation between seed length and fruit diameter in supplejack ($R^2 = 0.654$, $F = 220.6$, $P < 0.001$), a significant but extremely weak correlation in kohekohe ($R^2 = 0.029$, $F = 4.96$, $P = 0.027$), and no correlation in tawapou (*Planchonella costata*; $R^2 = 0.002$, $F = 0.227$, $P = 0.635$). For supplejack, we used seed length to predict fruit diameter (regression equation: $-1.2160 + 1.7092x$). For kohekohe seed diameter was the best predictor available. We were unable to predict tawapou fruit diameter from undispersed tawapou seeds. We therefore excluded tawapou from the ANOVA for differences in seed diameter among dispersed and undispersed fruits and from

the analysis of the effect of mean seed diameter on fruit size preference across plant species.

Seven of the 12 species/site/year collections tested showed a statistically significant difference in seed diameter among dispersed and undispersed fruits (Table 7.3). The diameter of dispersed seeds was smaller than average in four plant species, and larger than average in three species. Measured differences between dispersed and undispersed seeds were generally less than one millimetre.

Although dispersed supplejack seeds were significantly smaller in diameter than undispersed seeds, they were also significantly longer ($F = 51.22$, $P < 0.001$, Table 7.3). Seed length was more strongly correlated with fruit diameter than was seed diameter, so birds appear to have selected larger fruits.

Across all plant species we found no support for our hypothesis that the degree of preference for large fruits in pigeons was negatively correlated with species mean fruit size. There was no correlation between mean fruit diameter and fruit size preference ($R^2 = 0.00427$, $F = 1.047$, $P = 0.3303$, Figure 7.1). We also examined the relationship using the measured size of dispersed seeds and results agreed with those using estimated fruit size ($R^2 = 0.01031$, $F = 0.1042$, $P = 0.7535$).

Table 7.2 Relationship between fruit diameter and seed diameter of undispersed fruits in all of the studied plant species. For multi-seeded species regressions were carried out using all seeds from both single-seeded and multi-seeded fruits. P-values in bold indicate a regression slope significantly different from zero. Region abbreviations: 1 = Northland, 2 = Canterbury, 3 = Kaikoura, 4 = Kapiti.

Species	Region	Year	Regression equation	R^2	F	df	P
Single-seeded spp.							
karaka	1	2005	0.4923 + 1.2213 *x*	0.677	205.2	98	**0.0001**
ngaio	2	2005	2.9434 + 1.1847 *x*	0.541	115.7	98	**0.0001**
nikau	2	2005	4.1739 + 0.6562 *x*	0.417	69.94	98	**<0.001**
pigeonwood	3	2005	1.7260 + 0.9279 *x*	0.821	450.4	98	**0.0001**
pigeonwood	1	2005	0.6518 + 1.0823 *x*	0.803	399.9	98	**0.0001**
swamp maire	4	2006	6.52555 + 0.72883 *x*	0.527	109.1	98	**0.0001**
taraire	1	2005	5.9194 + 0.8640 *x*	0.652	183.5	98	**0.0001**
tawa	3	2004	3.6326 + 0.9821 *x*	0.526	108.7	98	**0.0001**
tawa	3	2005	-1.9714 + 1.5249 *x*	0.697	341.4	148	**0.0001**
tawa	3	2006	5.9860 + 0.8295 *x*	0.529	110.0	98	**0.0001**
Multi-seeded spp.							
kohekohe	1	2005	4.2983 + 0.6834 *x*	0.244	52.9	164	**<0.001**
supplejack	3	2005	3.8720 + 0.9121 *x*	0.254	39.84	117	**<0.001**
tawapou	1	2005	22.878 - 0.3837 *x*	0.009	1.166	123	0.282

Table 7.3 Comparison of seed sizes for dispersed and undispersed fruits. We present the mean diameter and length of seeds (and, for undispersed fruits, of fruits), and results of ANOVA comparing seed diameter in undispersed vs. dispersed seeds. All measurements are in millimetres. The ANOVA excluded tawapou, for which there was no significant correlation between seed diameter and fruit diameter. P-values in bold indicate a significant difference between dispersed and undispersed seed diameters. Where the F-test was significant the larger mean seed diameter is indicated in bold. Region abbreviations: 1 = Northland, 2 = Canterbury, 3 = Kaikoura, 4 = Kapiti.

			Undispersed					**Dispersed**		**ANOVA comparing seed diameters**		
Species	Region	Year	No. seeds per fruit	Fruit diam.	Fruit length	Seed diam.	Seed length	Seed diam.	Seed length	F	df	P
karaka	1	2005	1	20.1	28.2	**16.1**	24.8	15.1	23.3	9.72	1, 139	**0.002**
kohekohe	1	2005	1–3	9.0	18.4	7.2	11.3	**8.0**	11.3	65.47	1, 264	**<0.001**
ngaio	2	2005	1	8.0	8.8	4.3	7.7	4.4	8.0	3.00	1, 198	0.085
nikau	2	2005	1	9.5	13.5	**8.1**	13.3	7.5	12.6	77.32	1, 156	**<0.001**
pigeonwood	1	2005	1	9.7	13.8	8.3	12.0	**8.6**	12.0	7.52	1, 198	**0.007**
pigeonwood	3	2005	1	9.2	13.6	**8.1**	12.2	7.3	11.1	121.32	1, 198	**<0.001**
supplejack	3	2005	1–4	10.8	12.0	**8.1**	7.3	6.9	8.2	109.45	1, 217	**<0.001**
swamp maire	4	2006	1	13.1	13.1	9.0	11.9	9.3	11.8	2.26	1, 163	0.134
taraire	1	2005	1	19.4	31.6	15.6	29.3	15.5	28.6	0.14	1, 168	0.707
tawa	3	2004	1	14.5	24.5	11.1	23.5	11.3	23.3	1.45	1, 159	0.231
tawa	3	2005	1	15.7	24.3	11.6	22.6	**12.2**	24.3	8.54	1, 248	**<0.001**
tawa	3	2006	1	16.1	27.4	12.1	26.5	11.9	25.4	3.54	1, 198	0.061
tawapou	1	2005	1–5	17.5	29.5	10.3	23.8	10.4	24.2	—	—	—

Table 7.4 Fruit diameter, disperser gape widths and relative size of dispersed versus undispersed fruits for published studies investigating fruit size preferences in avian dispersers.

Study	Plant species	Fruit diam. range (mm)	Dispersers (gape width in mm)	Relative size
Wheelwright 1993	*Ocotea tenera*	14.1-23.7	*Pharomachrus mocinno* (21.0†) *Procnias tricarunculata* (25.0†) *Aulacorhynchus prasinus* (26.0†) *Ramphastos sulphuratus* (31.0†) *Chamaepetes unicolor* (31.0†)	Larger
Alcantara & Rey 2003	*Olea europea var. sylvestris*	5.25-10.2‡	*Turdus philomelos* (13.7§) *Sylvia atricapilla* (8.5§) *S. melanocephala* (7.1§) *Erithacus rebecula* (8.0§)	Smaller
Parciak 2002	*Prunus virginiana*	Not reported	*Bombycilla cedrorum* (—) *Turdus migratorius* (—)	Smaller
Howe and Vande Kerckhove 1981	*Virola surinamensis*	Not reported	*Penelope purpurascens* (—) *Trogon massena* (—) *Baryphthengus martii* (—) *Pteroglossus torquatus* (—) *Rhamphastos swainsonii* (—) *R. sulphuratus* (31.0†) *Tityra semifasciata* (18.0†) *Ateles geoffroyi* (—)	Smaller
Sallabanks 1993	*Crataegus monogyna*	Not reported	*Turdus migratorius* (—)	Larger
This study	*Beilschmiedia tawa (2004)*	11.1-17.6	*Hemiphaga novaeseelandiae* (25.0††)	No difference
	B. tawa (2005)	11.5-20.3		Larger
	B. tawa (2006)	12.9-19.0		No difference
	B. tarairi	14.6-22.6		No difference
	Corynocarpus laevigatus	12.0-31.1		Smaller
	Hedycarya arborea (N)	8.1-11.4		Larger
	H. arborea (K)	8.0-10.5		Smaller
	Myoporum laetum	6.2-10.5		No difference
	Rhopalostylis sapida	8.3-9.5		Smaller
	Ripogonum scandens	6.2-13.0		Larger

†Gape widths from Wheelwright (1985); ‡fruit dimensions from Rey et al. (1997), estimated from graph; §gape widths from Herrera (1984); ††swallowing limit due to distensible gape (Gibb 1970).

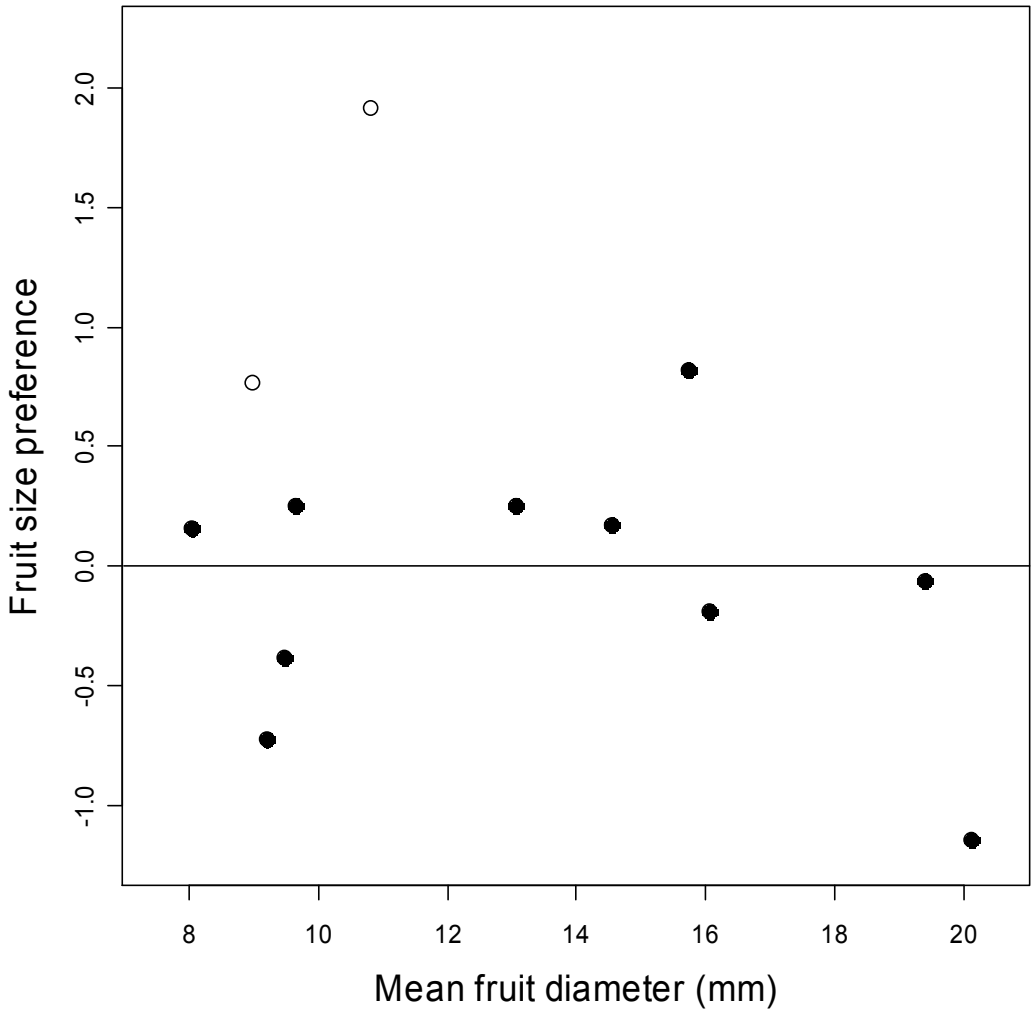

Figure 7.1 Overall correlation between mean fruit diameter and fruit size preference by New Zealand pigeons. Fruit size preference was calculated by subtracting the mean undispersed fruit diameter from the mean estimated dispersed fruit diameter for each plant species. Values greater than zero indicate a preference for larger than average fruit, and values less than zero represent a preference for smaller than average fruit. All species for which fruit diameter could be predicted from dispersed seeds were included in the analysis. Single-seeded species are represented by filled circles, and multi-seeded species by open circles. The relationship was non-significant (P = 0.3303).

7.5 Discussion

Our results demonstrate that there was no pattern to fruit size preferences by the New Zealand pigeon across plant species, populations, and years. This indicates that factors other than size were also, or mainly, influencing fruit choice. Gibb (1970) reported that accessibility, ripeness, and size all influenced fruit choice by New Zealand pigeons feeding on introduced plums. One potential bias of our study is that we cannot be certain that all dispersed seeds were deposited by pigeons. If other birds dispersed any of these seeds it may have influenced the size of fruits selected and any interference in selection patterns would be biased towards species with smaller fruits (for which more dispersers were available). However, based on our observations and published data on available dispersers (Clout & Hay 1989) we believe that ngaio was the only species that may have been dispersed in any significant quantity by alternative frugivores at the site and time of collection. Another potential source of bias is that we sampled undispersed fruits from the ground rather than directly from trees. This may have affected our results if fruits fell or were dropped non-randomly, compared to undispersed fruits that remained on the tree.

Although the differences in fruit size we observed among dispersed and undispersed seeds were small, the relative difference in reward may have been disproportionate. Wheelwright (1993) reported that a 6% increase in fruit diameter resulted in an 18% increase in fruit pulp. However, this does not necessarily correspond with a direct increase in the pulp to seed ratio (Wheelwright 1993), although it may be more likely for single-seeded species (Jordano 1992).

Results from the literature appeared to be consistent with our overall hypothesis that birds will prefer larger fruits when gape limitation is absent and smaller fruits when gape limitation is present. Other studies have reported a preference by avian frugivores for both smaller than average fruits (Howe & Vande Kerckhove 1981; Jordano 1995b; Parciak 2002; Alcantara & Rey 2003) and larger than average fruits (Sallabanks 1993; Wheelwright 1993; Table 7.4). We were unable to assess the presence of gape limitation in all of these studies, as gape width and fruit diameter range were not always reported. Where large fruits were dispersed more frequently (Wheelwright 1993), frugivores were large relative to fruits and gape limitation was present in only one of the five available dispersers (Wheelwright 1985, 1993). Where smaller fruits were more likely to be dispersed (Alcantara & Rey 2003), the gape widths of three of the four available avian

dispersers were too small to enable them to swallow the largest fruits (Herrera 1984; Rey et al. 1997). Across plant species, consumption rates by gape-limited sylviid warblers decreased with increasing fruit size (Jordano 1987).

Jordano (1995b) reported that dispersed seeds had a smaller mass than undispersed seeds. However, sampling was undertaken at different times, with undispersed seeds collected at the start of the fruiting season and dispersed seeds just after the ripe fruit crop had been exhausted by frugivores (Jordano 1995b). Fruits produced later in the season are typically smaller than those produced earlier, as resource availability declines (references in Parciak 2002).

The New Zealand pigeon is generally not gape-limited when feeding on the native flora (though it can be for example on introduced plums; Gibb 1970). The pigeon's ability to swallow fruits up to 25 mm in diameter (Gibb 1970) and the relatively small size of fruits in the New Zealand flora (Lord 2004) mean that limits to ingestion are generally absent; only in the largest fruits of karaka did gape limitation occur. Karaka fruits and seeds were used historically by Maori and planted around settlements (Costall et al. 2006). Maori may have preferentially cultivated karaka trees that produced larger fruits, providing a countervailing selection force to that which may be imposed by pigeon preferences for smaller fruit.

Although fruit size has been demonstrated to be heritable in at least some species (Wheelwright 1993; Cheng et al. 2004), it is thought to be an historic adaptation to disperser selection that is currently maintained by phylogenetic inertia and/or developmental constraints (Jordano 1995a). New Zealand fruits are relatively small compared to Australian and South American congenerics, and become more elliptical with increasing fruit size (Lord 2004). Both these traits provide evidence for historical adaptation of New Zealand fruits to the comparatively small-bodied avian disperser assemblage (Lord 2004). The pigeon has probably always been the most important frugivore in New Zealand, due to its large size, ability to fly long distances, and highly frugivorous diet. However, there is only limited information on the diet of extinct birds, and it is not possible to determine whether they exerted any selection pressure on fruit size evolution in New Zealand. As fruit selection by the New Zealand pigeon is generally not constrained by fruit size, any preferences should reflect variation in other fruit and plant traits present in individual plant species.

Chapter 8. Synthesis

The main objectives of this thesis were to assess the effectiveness of kereru as seed dispersers, and to determine the importance of kereru seed dispersal for regeneration of large-seeded tree species. This chapter synthesises the main research findings with information from other studies to address these objectives, and discusses potential future research directions.

8.1 Effectiveness of kereru as seed dispersers

Seed disperser effectiveness is defined as the contribution a disperser makes to a plant's future reproduction, and has both quantitative and qualitative components (Schupp 1993). Seed dispersal quantity depends on the number of visits a disperser makes, and the number of seeds dispersed per visit (Schupp 1993). Dispersal quality depends on the treatment of seeds in the disperser's mouth and gut, and on seed deposition patterns (Schupp 1993).

8.1.1 Dispersal quantity

Kereru are primarily frugivorous, consuming fleshy fruits from more than 70 plant species (McEwen 1978; Clout & Hay 1989). Kereru in the Auckland region fed on fruit in 90% of feeding observations, while foliage and flowers made up the remaining 10% of observations (Dijkgraaf 2002). For each species, the proportion of available fruits that kereru consume appears to depend on differences in fruit palatability among plant species. Kereru at Pelorus Reserve in Marlborough consumed huge quantities of miro fruits (which are a preferred food) over the course of the fruiting period (Clout & Hay 1989). Only a small proportion of available karaka fruits are eaten, indicating that kereru do not favour this species (Powlesland et al. 1997; Dijkgraaf 2002).

Kereru fruit removal rates have generally not been quantified, although Clout & Hay (1989) reported one kereru that removed 98 miro fruits per day (and nearly 10,000 fruits over the four month fruiting period) from a single miro tree. This kereru is estimated to have taken 85% of the total fruit crop from one miro tree, which it defended successfully against other birds (Clout & Hay 1989). Kelly et al. (2006) found that kereru made 17% of all fruiting plant visits across a range of mostly small-fruited species. They were the third most important disperser numerically across all plant species, after silvereyes and bellbirds. In seven of 39 cases kereru made more than 50% of all visits, including for miro

in South Westland, where they made 93.7% of visits. Dijkgraaf (2002) reported the number of ingested seeds and whole fruits collected from seed traps beneath parent trees at six Auckland sites. Kereru consumed 11% of karaka fruits collected in traps, 31% of puriri fruits, 36% of taraire fruits, 34% of tawa fruits, and 50% of kohekohe fruits (Dijkgraaf 2002). The actual proportion of the total fruit crop consumed was probably much higher, as kereru deposit 66–87% of ingested seeds away from parent trees (Table 3.1, Chapter 3), which would not have been collected in seed traps beneath parents. Nevertheless, this data may give an idea of the relative fruit removal rates among large-seeded species, although the proportion of ingested seeds deposited beneath parents can differ among species (see below).

8.1.2 Dispersal quality

Kereru defecate seeds intact and seed treatment in the gut is gentle, sometimes enhancing germination by fruit pulp removal and/or seed scarification (e.g. taraire; Chapter 4; Myers 1984; Bell 1996). Kereru ingestion of miro seeds had no effect on germination success compared to whole fruits, but this species has recalcitrant seeds that can take over four years to germinate (Clout & Tilley 1992).

Although kereru were highly sedentary at times, remaining up to five and a quarter hours at a single location with a mean residence time of 32 minutes (Chapter 3), seed retention times were relatively long (mean range 37–181 minutes; Clout & Tilley 1992; Wotton et al. in press). Thus, for most plant species kereru defecated the majority of seeds away from the parent tree (Chapter 3; Clout & Tilley 1992; Bell 1996), which increased the probability of survival in at least some large-seeded species (Table 5.5, Chapter 5). Kereru were estimated to disperse 66% of fivefinger seeds, 87% of tawa and puriri seeds (Table 3.1, Chapter 3), and 65% of miro seeds away from parent plants (Clout & Tilley 1992).

Bell (1996) quantified kereru seed deposition patterns for nikau, kahikatea, taraire, and puriri. Kereru defecated nearly 50% of puriri seeds beneath puriri trees, but only around 10–20% of nikau, kahikatea, and taraire seeds beneath conspecific adults (Bell 1996). Defecation patterns were related to variation in kereru behaviour among tree species, with birds most likely to remain in the same tree after feeding on puriri (63% of observations; Bell 1996). In nikau, kereru remained in the same tree after feeding only 9% of the time and rarely moved to a new nikau tree (Bell 1996). Bell's findings are consistent with the results from my research, which showed variation in residence times among tree

species (Table 3.2, Chapter 3). For taraire and kahikatea, kereru were also highly likely to depart trees after feeding (69% and 79% of observations respectively), and moved to conspecific trees only 13–14% of the time (Bell 1996). Kereru resting sites appear to be influenced by tree architecture, and are generally on large branches (presumably for increased comfort and stability) sheltered by the canopy, which may reduce the risk of avian predation (Bell 1996). Kereru are also more likely to deposit seeds of all species in the forest interior than in gaps and forest edges (Bell 1996).

In this study, kereru dispersed 79–88% of seeds up to 100 m from the source and less than 1% of seeds up to c. 1,500 m (Table 3.1, Chapter 3). These dispersal distances are comparable to those reported by Clout and Tilley (1992) for an individual kereru that dispersed 40% of seeds 10-30 m away, and < 2% over 1 km from the source. Because large seeds take longer to pass through the kereru's gut than small seeds (Wotton et al. in press), they have the potential to be dispersed longer distances (Chapter 3). Kereru can move distances of tens of kilometres (Clout et al. 1986; Clout et al. 1991), sometimes in a single flight (Harper 2003), and probably disperse seeds this far on occasion.

Kereru appear to deposit seeds at varying densities, depending on the fruit species and individual perching patterns, although seed density deposition patterns have not been quantified. The number of seeds contained in a defecation appears to increase with decreasing seed size. Kereru defecated the largest seeds (e.g. tawa, taraire, and karaka) singly, and the slightly smaller seeds of miro and puriri one to three seeds at a time (Wotton et al. in press). Medium-sized seeds such as nikau were often found at moderate densities (DMW personal observation), while more than 60 seeds of the small-seeded mahoe were counted in a single defecation (DMW personal observation). Some kereru have favoured roosting or perching sites, beneath which large piles of seeds can accumulate (DMW personal observation; Figure 8.1). The effects of seed density on survival differed between species, with negative density-dependent mortality in karaka and positive density-dependent mortality in taraire (Table 5.5, Chapter 5). However, when kereru deposit very large piles of conspecific seeds under a favoured perch the effects on seed survival seem certain to be negative.

Kereru provide effective seed dispersal by consuming large quantities of fruit, enhancing or having no effect on germination success, and depositing most seeds away from the parent (which enhances survival in at least some species) at distances up to at least 1,500 m and probably occasionally tens of kilometres. Dispersal effectiveness appears

to differ among fruit species, reflecting differences in both the time kereru spend in feeding trees and seed retention times.

Figure 8.1 Large pile of seeds defecated beneath a kereru roost (Photo: Dave Kelly).

8.2 Importance of kereru as dispersers of large-seeded trees

8.2.1 Consequences of dispersal failure

Kereru densities have declined significantly since the arrival of humans (Pierce et al. 1993), which may have decreased both the proportion of seeds dispersed and dispersal distances, and increased the proportion of ingested fruits deposited beneath parents. High kereru densities appear to decrease kereru residence times in fruiting trees and increase the frequency of movements between forest patches due to increased competition for fruit (Clout et al. 1991).

There are five widely recognised, large-seeded tree species for which kereru are virtually the sole disperser: tawa, taraire, puriri, karaka, and tawapou (Clout & Hay 1989). Dispersal failure decreased the probability of survival during the first two years by 60–93% for two of these species (karaka and taraire, Figure 5.10, Chapter 5). Puriri may also be vulnerable to dispersal failure, as it appears unable to regenerate beneath its own canopy (Campbell & Atkinson 1999). Puriri is bird-pollinated as well, which may make it

particularly susceptible to mutualism disruption. However, puriri is capable of producing some viable seeds from self-pollinated flowers (Barrell et al. 1997), and puriri pollination may be adequate where tui are still common, as seems likely through most of the plant's natural range (northern New Zealand; Higgins et al. 2001). There are no published data on pollination rates in puriri.

Depressed seedling recruitment resulting from dispersal failure may ultimately lead to inadequate regeneration in large-seeded tree species and subsequent changes in forest composition. Any effects will be most prevalent in the North Island of New Zealand, where large-seeded species dominate many forests.

8.2.2 Potential replacement dispersers

The five large-seeded tree species that reportedly rely on kereru for dispersal are sometimes eaten by other bird species (Table 6.1, Chapter 6). Although dispersal by birds other than kereru is likely to be uncommon, rare events can have a disproportionate influence on plant recruitment (Clark et al. 1998b; Jordano et al. 2007). Tui may provide effective dispersal, as they are much more mobile than kereru, with a mean residence time of only 11 minutes (O'Connor 2006). Tui fly comparable distances to kereru, with frequent flights of, and estimated dispersal of seeds to, 1–200 m (O'Connor 2006) and daily movements of up to 30 km (Bergquist 1985). Large-seeded plants also may have rare long distance dispersal by means other than birds, including water, inside and outside naturalised mammals such as pigs, sheep, cattle and horses, and accidental transport by humans (e.g. in dirt on vehicles). Such processes are hardly studied (Williams et al. 2000; Williams 2003).

The dispersal of smaller-than-average tawa seeds (the ones alternative dispersers are capable of swallowing) appears to result in decreased seedling size through the first two years (Figures 6.3 and 6.4, Chapter 6). To what extent this reduces the long-term probability of seedling survival in the field remains to be seen.

8.3 Future research directions

To fully assess the effectiveness of kereru as seed dispersers, quantitative data on fruit removal rates and seed deposition densities should be collected. Some of the mechanisms for decreased survival of undispersed seeds in karaka and taraire remain unknown, and could provide an interesting follow-up to this study. In particular, although some of the

reduced survival under parents was explained by mammals targeting fruiting trees, the remaining decrease was unexplained. A range of potential factors could have caused this decrease, including host-specific pathogens, allelopathy, and the presence of deep and persistent litter beneath parents. The consequences of dispersal failure also need to be assessed experimentally for other large-seeded tree species, especially puriri, tawa, and tawapou.

The potential for other bird species and introduced mammals to effectively disperse large seeds needs to be quantified. Systematic feeding observations combined with collection of droppings will enable an assessment of dispersal quantity by alternative species. Dispersal quality should be determined as well, by comparing germination success of ingested and uningested seeds. If some viable seeds are defecated, deposition patterns (including dispersal distance), and their effect on subsequent recruitment should also be quantified. The consequences of dispersal of smaller-than-average seeds by potential replacement dispersers should be tested in the field.

One of the key benefits of kereru seed dispersal may be the maintenance of human-fragmented metapopulations of large-seeded tree species. Much of New Zealand's remaining forest habitat occurs in relatively small and isolated patches. Because trees are relatively long-lived, a modelling approach may be the most useful in elucidating the effects of kereru density and landscape structure on seed dispersal between patches and metapopulation maintenance. Seed dispersal is also important for local genetic structure and gene flow among populations (García et al. 2007) and genetic methods may be useful in estimating past rates of movement of seeds among populations. Inbreeding appears to be particularly detrimental in large-statured plants (trees and shrubs), with complete mortality of inbred offspring prior to maturity (Scofield & Schultz 2006). Thus, fragmented tree populations may be particularly vulnerable to extinction (Scofield & Schultz 2006) even if the long generation times mean that this would take many years to eventuate. The genetic consequences of seed dispersal and forest fragmentation in New Zealand are currently unknown. Nevertheless, kereru dispersal of seeds between forest patches may be essential in maintaining fragmented metapopulations of large-seeded trees.

Acknowledgements

A huge thanks to Dave Kelly for being such a wonderful supervisor and providing encouragement, support, and advice throughout my PhD. Your enthusiasm, insightful comments, and confidence in me are greatly appreciated and I feel privileged to have worked with you. Thanks also to my associate supervisor Mick Clout for all your advice during planning the thesis and feedback on chapters. I greatly appreciate your time and expertise.

Thanks heaps to Jenny Ladley for all your help, including organising equipment, assisting with fieldwork, and for providing advice and moral support throughout. I'm grateful to Maggie Tisch for providing logistical support and helping me with the kereru radio-tracking – thanks for your energy, positive attitude, and wonderful company. Thanks to Matt Walters for all your help with photography and graphical design, and to Dave Conder for assistance at the glasshouses. Thanks also to Roger Dungan for many useful discussions and for providing statistical advice.

Thanks to Chris Berry, Dean Benvenuti, Javi Rodríguez, Bev Woods, Reuben Ferguson, and Sue Molloy for assistance with field work. I am grateful to Richard Duncan and Ashley Sparrow for statistical advice on the seed fate experiment, John Thyne for calculating the kereru location distances in ArcInfo, and Robbie Holdaway who helped write the R code for the seed dispersal model.

I am indebted to the Auckland Regional Council for supporting this research in so many ways: for giving permission to conduct research at Wenderholm Regional Park, funding, accommodation, and logistical support. Thanks in particular to Tim Lovegrove, Ngaire Sullivan, Sue Hill, Ross Gaastra, Barry Green, and all the duty rangers at Wenderholm. Thanks also to Ray Pierce for giving permission to conduct research on his property and for all the support provided. Wellington City Council, Kathy and Don Hutchinson, Nga Manu Reserve, Department of Conservation, Brian and Faye Narby, and other landowners around Hinewai, Akaroa, and New Plymouth also gave permission to conduct research on their properties. Orana Wildlife Park and Willowbank Wildlife Reserve kindly gave permission to conduct research on kereru in their aviaries.

Thanks to Ralph Powlesland at Department of Conservation for allowing me to radio-track kereru in Taranaki and for advice on kereru. Thanks also to Kirsty Moran and Sarah Kivi at DoC for showing me where to find radio-tagged kereru in Taranaki and all

your support during fieldwork there. Kirsten Campbell showed me how to radio-track kereru and let me follow her radio-tagged birds, for which I am grateful. Thanks also to Kerry-Jayne Wilson at Lincoln University for permission to track kereru on Banks Peninsula and for useful advice. Hugh Wilson kindly gave permission to conduct research at Hinewai Reserve and provided accommodation. Thanks to John Innes at Landcare Research for the loan of radio-tracking equipment.

Dean Benvenuti, Ronny Groenteman, Melissa Hutchison, Laura Young, and Lisa Berndt provided much appreciated moral support and encouragement throughout my PhD. Kim McConkey, Alistair Robertson, Doug Levey and an anonymous reviewer provided helpful comments on earlier drafts of the fruit size preference chapter. Thanks to all the people who provided information and showed me around when I was looking for field sites, especially Nan Pullman of QEII Trust, and John and Cathy Hawley for your hospitality at Marunui. Sandra Anderson kindly provided unpublished data on bird gape widths, Jo Ward identified cherry laurel, Richard Holdaway provided information on moa and other bird stuff, and Robert Hoare identified karaka insect seed predators.

I am grateful to all the organisations that provided financial assistance, including grants from the Foundation for Research Science and Technology (contract C09X0503), Auckland Regional Council, Brian Mason Scientific and Technical Trust, University of Canterbury, Robert C. Bruce Trust, and Canterbury Botanical Society. I was supported by a University of Canterbury Doctoral Scholarship, a New Zealand Federation of Graduate Women Fellowship, and a Royal Forest and Bird Protection Society (North Canterbury Branch) Stocker Scholarship. This research was conducted with University of Canterbury Animal Ethics Committee approval.

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Appendix I. Dispersal model

Written by Robbie Holdaway and Debra Wotton

```
# R script to estimate seed dispersal kernals, using kereru radio-
tracking movement data and seed retention times.

# Four kereru tracking sessions (birddays) were excluded (one session was
less than the longest seed retention time and has missing values, and
three other birddays have missing values. The analysis uses 39 birddays.
Each birdday is assigned a different sequential number from 1 to 39
("bcount" in the model).

# the model randomly generates 100 seed retention times, from a normal
distribution using a specified mean and standard deviation (from actual
data for each plant species).

# The model then calculates the dispersal distance for each of the 100
seeds for each minute of each birdday.

# To start a session, bring up a function window:

fix(disp.function)

# copy and paste function code in

function(time = 180.8,timesd = 100.3,guttimerep=100){      # the default
values are for tawa

  # read in movement file. Note all data with NA time arrived/departed
values (except at start and end of birdday should be removed from mvmt
data file before loading into R

setwd("D:\\PhD thesis\\kereru mvmts\\data")
  mvmt<-read.table("mvmt.no.na.txt", header=T, sep="\t")
  mvmt$bird<-factor(mvmt$bird)
  attach(mvmt)

  # calculating the minutes spent in each location (aka the mins column
of mvmt!!!)

residence<-rep(NA,dim(mvmt)[[1]])

  for(i in 1.:dim(mvmt)[[1]]){

# for the first location in each tracking session the residence time is
the departure time minus the arrival time

if(seq[i] == 1){
        residence[i]<-mvmt$mins.dep[i]-mvmt$mins.loc[i]
    }

# for the last location in each tracking session, the residence time is
time located minus the departure time from the previous location

if(seq[i+1]==1 & i !=dim(mvmt)[1] & seq[i]!=1){
      residence[i]<-mvmt$mins.loc[i]-mvmt$mins.dep[i-1]
    }
```

```
# for all other vlues the residence time is the time departed at that
location minus the time departed from the previous location

if(seq[i]!=1){
      residence[i]<- mvmt$mins.dep[i]-mvmt$mins.dep[i-1]
    }
  }

# gut time distribution
    # randomly generate 100 seed retention times, from a normal
distribution using a specified mean and standard deviation
    # the loops remove negative values

guttime<-rnorm(guttimerep,mean=time, sd=timesd)
  for(i in 1:guttimerep){
  if(guttime[i] <0){
    guttime[i]<-rnorm(1,mean=time, sd=timesd)
    }
  }
  for(i in 1:guttimerep){
  if(guttime[i] <0){
      guttime[i]<-rnorm(1,mean=time, sd=timesd)
      }
  }

# for a set guttime, for each minute of each birdday, calcuate possible
dispersal distances
# First create the output array - note the final length varies so create
it big enough to handle all possible values
# rounding is used to get integers
disp.kernal<-array(data = NA, dim =
c(length(guttime),nlevels(bird.day),round(600-min(guttime))))

# set working directory to enable distance files to be read in:
setwd("D:\\PhD thesis\\kereru mvmts\\data\\distances\\dist txt")

# The big loop...
  guttimecount<-0

  # for each of the seed retention times
    for(j in 1:guttimerep){

  # use the radmonly generated gut times, rounded to the nearest integer
    guttime.value<-round(guttime[j])
    guttimecount<-guttimecount+1

  # print the gut time count on screen so I know where the loop is up to
    print(guttimecount)
    bcount<-0

  # for each of the bird days:
    for(b in levels(bird.day)){
      bcount<-bcount+1
      # print the bird count on screen so I know where the loop is up to
        print(bcount)

      # calculate the number of minutes from start of tracking session
      residence.sum<-cumsum(residence[bird.day == b])

      # the location where fruit is eaten
```

```
      bird.location<-pt[bird.day == b]

      # the end time for the bird day
      endtime<-max(residence.sum,na.rm=TRUE)
      # the final eating time for which seed dispersal distance will be
calculated is the point at which the minutes remaining
        # for that bird day is less than or equal to the seed retention
time for the jth seed.
      length.test<-residence.sum<=(endtime-guttime.value)
      if(length.test==TRUE){
      final.eating.time<-
residence.sum[max(which(residence.sum<=round(endtime-guttime.value)))]

                # for each minute of each birdday
        for(t in 1:(final.eating.time-1)){
          # determine the eating location
          bird.start.position<-
bird.location[min(which(residence.sum>=t))]
          # determine the defecation location
          bird.end.position<-
bird.location[min(which(residence.sum>=(t+guttime.value)))]
          # load the distance file for that bird
          dist.file<-read.table(b, header=T, sep="\t")
          # calculate the seed dispersal distance
          disp.kernal[j,bcount,t]<-
dist.file$distance[dist.file$pt1==bird.start.position &
dist.file$pt2==bird.end.position]
                }
      }
    }
  }

# create frequency distribution of seed dispersal distances
  dist.hist<-hist(disp.kernal,breaks=100)
# and draw a scatterplot with a line from the frequency data
  plot(dist.hist$counts/(length(disp.kernal)-
summary(disp.kernal)[7])~dist.hist$breaks[2:length(dist.hist$breaks)],
xlab = "Distance dispersed (m)", ylab = "Probability", type="l")

# save the seed dispersal distances and gut times as objects
  list("disp.kernal" = disp.kernal,"guttimes"=guttime)
}



# for each plant species type the following to change the default values
for mean and standard deviation seed retention time, and number of seed
retention times to use and run the function and save output to
object.name:
  tawa<-disp.function(time =180.8,timesd =100.3, guttimerep = 100)

# to save the seed dispersal distances and gut times objects as an
external file
  save(tawa, file = "D:\\PhD thesis\\kereru mvmts\\data\\tawa
dispersal.Rdata")

  # to reload the data
  load("D:\\PhD thesis\\kereru mvmts\\data\\tawa dispersal.Rdata")
```

Appendix II. Seed fate models

Generalised linear mixed models explaining variation in total seed predation, germination, one year survival, two year survival, and seedling height growth. The explanatory variables were fruit (whole fruit or clean seeds), density (seed density high, 20 seeds or low, 4 seeds), cage (mammal exclusion or open access), and location (under parent or 20 m away). All models also contained the random effects of plots nested within parent trees. For each model, the log likelihood, Akaike information criterion (AIC) and ΔAIC (the difference in AIC between a model and the best-fitting model with the lowest AIC score) are shown. Models listed are those with substantial support (ΔAIC ≤2 compared to the best-fitting model).

Table 1. Models explaining variation in total seed predation (including insect predation, mammal predation and removed seeds). Seed predation was modelled using a binomial distribution. (a) taraire, (b) karaka Mt Tiger, (c) karaka Wenderholm.

(a)

model	log likelihood	No.	AIC	ΔAIC
fruit + density + cage + loc + fruit:density + fruit:loc + density:cage	-77.891	14	173.782	0
fruit + density + cage + loc + fruit:density + density:cage	-79.037	18	174.073	0.291
fruit + density + cage + loc + fruit:density + fruit:cage + fruit:loc + density:cage	-77.118	12	174.236	0.454
fruit + density + cage + loc + fruit:density + fruit:cage + density:cage	-78.274	15	174.547	0.765
fruit + density + cage + loc + fruit:loc + density:cage	-79.342	17	174.684	0.902
fruit + density + cage + loc + fruit:cage + fruit:loc + density:cage	-78.769	13	175.538	1.756
fruit + density + cage + loc + fruit:density + fruit:loc	-79.888	19	175.776	1.994

Table 1 cont.

(b)

model	log likelihood	No.	AIC	ΔAIC
fruit + cage + loc + fruit:cage + cage:loc	-79.292	22	172.584	0
fruit + cage + loc + fruit:cage + fruit:loc + cage:loc	-78.766	17	173.531	0.947
fruit + density + cage + loc + fruit:cage + cage:loc	-79.026	19	174.052	1.468

(c)

model	log likelihood	No.	AIC	ΔAIC
cage	-79.494	31	164.988	0
fruit + cage	-79.335	30	166.670	1.682
cage + loc	-79.432	28	166.864	1.876
fruit + cage + loc + fruit:loc	-78.74	23	169.5	4.512

Table 2. Models explaining variation in germination success for unpredated seeds. Seed germination was modelled using a binomial distribution. (a) taraire, (b) karaka Mt Tiger, (c) karaka Wenderholm.

(a)

model	log likelihood	No.	AIC	ΔAIC
fruit + density + loc + fruit:density + density:loc	-41.041	3	96.081	0
fruit + density + loc + fruit:density + fruit:loc + density:loc	-40.111	1	96.223	0.142
fruit + density + loc + fruit:density	-42.529	6	97.059	0.978

(b)

model	log likelihood	No.	AIC	ΔAIC
fruit + density + loc + fruit:density	-53.501	6	119.003	0
fruit + density + loc	-54.650	8	119.300	0.297
fruit + density + loc + fruit:density + density:loc	-53.261	3	120.522	1.519
fruit + density + loc + fruit:density + fruit:loc	-53.378	4	120.755	1.752
fruit + density + loc + density:loc	-54.443	5	120.886	1.883

(c)

model	log likelihood	No.	AIC	ΔAIC
fruit	-47.465	11	100.930	0
fruit + location	-46.734	9	101.468	0.538
Intercept	-48.740	12	101.480	0.55
location	-48.001	10	102.003	1.073
fruit + location + fruit:loc	-46.054	7	102.108	1.178

Table 3. Models explaining variation in survival to one year for germinated seeds. One year survival was modelled using a binomial distribution. (a) taraire, (b) karaka Mt Tiger, (c) karaka Wenderholm.

(a)

model	log likelihood	No.	AIC	ΔAIC
fruit + density + cage + loc + fruit:loc + density:cage + cage:loc	-47.464	13	112.929	0
fruit + density + cage + loc + fruit:loc + density:cage	-48.591	19	113.181	0.252
fruit + density + cage + loc + fruit:cage + fruit:loc + density:cage	-47.942	16	113.884	0.955
fruit + density + cage + loc + fruit:cage + fruit:loc + density:cage + cage:loc	-47.079	8	114.158	1.229
fruit + density + cage + loc + density:cage + cage:loc	-49.212	17	114.424	1.495
fruit + density + cage + loc + fruit:density + fruit:loc + density:cage + cage:loc	-47.417	9	114.835	1.906

(b)

model	log likelihood	No.	AIC	ΔAIC
fruit + density + cage + loc + fruit:cage + fruit:loc	-94.305	20	204.610	0
fruit + density + cage + loc + fruit:loc	-95.809	22	205.619	1.009
fruit + density + cage + loc + fruit:cage + fruit:loc + cage:loc	-94.079	13	206.159	1.549
fruit + density + cage + loc + fruit:density + fruit:cage + fruit:loc	-94.142	16	206.284	1.674
fruit + density + cage + loc + fruit:cage	-96.273	23	206.546	1.936

Table 3 cont.

(c)

model	log likelihood	No.	AIC	ΔAIC
fruit + density + cage + loc + fruit:cage + fruit:loc + density:loc	-92.423	16	202.845	0
fruit + density + cage + loc + fruit:cage + fruit:loc	-93.658	19	203.315	0.47
fruit + density + cage + loc + fruit:cage + fruit:loc + density:loc + cage:loc	-91.723	10	203.446	0.601
fruit + density + cage + loc + fruit:cage + fruit:loc + cage:loc	-92.937	15	203.875	1.03
fruit + density + cage + loc + fruit:cage + fruit:loc + density:cage + density:loc	-92.276	12	204.552	1.707

Table 4. Models explaining variation in survival from one to two years for karaka at both sites. Two year survival was modelled using a binomial distribution.

model	log likelihood	No.	AIC	ΔAIC
density + loc	-148.03	9	304.07	0
density + loc + density:loc	-147.48	7	304.97	0.9
density + loc + site	-148.03	8	306.06	1.99

Table 5. Models explaining variation in seedling height to one year for germinated seeds. Seedling height was modelled using a Gaussian distribution. (a) taraire, (b) karaka Mt Tiger, (c) karaka Wenderholm.

(a)

model	log likelihood	No.	AIC	ΔAIC
fruit + density + cage + loc + fruit:loc + density:cage	-185.97	19	387.94	0
fruit + density + cage + loc + fruit:loc + density:cage + cage:loc	-185.24	13	388.48	0.54
fruit + density + cage + loc + fruit:loc	-187.35	21	388.71	0.77
fruit + density + cage + loc + density:cage	-187.46	20	388.91	0.97
fruit + density + cage + loc + density:cage + cage:loc	-186.52	17	389.04	1.1
fruit + density + cage + loc + fruit:loc + cage:loc	-186.58	18	389.16	1.22
fruit + density + cage + loc + fruit:cage + fruit:loc + density:cage	-185.77	16	389.55	1.61
fruit + density + cage + loc + fruit:cage + fruit:loc + density:cage + cage:loc	-184.86	11	389.71	1.77

(b)

model	log likelihood	No.	AIC	ΔAIC
fruit + cage + loc + fruit:cage	-330.83	22	673.67	0
fruit + cage + loc	-332.50	26	675.00	1.33
fruit + density + cage + loc + fruit:cage	-330.79	21	675.58	1.91

(c)

model	log likelihood	No.	AIC	ΔAIC
density + loc + density:loc	-365.79	25	741.58	0
density + loc	-366.91	27	741.82	0.24
fruit + density + loc + density:loc	-365.73	23	743.47	1.89

Table 6. Models explaining variation in seedling growth from year one to year two for karaka. Growth was modelled using a Gaussian distribution. (a) karaka Mt Tiger, (b) karaka Wenderholm.

(a)

model	log likelihood	No.	AIC	ΔAIC
cage + location + cage:location	-289.00	7	588.01	0
cage + location	-290.13	9	588.25	0.24
density + cage + location + cage:location	-288.98	5	589.95	1.94

(b)

model	log likelihood	No.	AIC	ΔAIC
density + cage + density:cage	-339.24	7	688.48	0
density + cage	-340.55	9	689.11	0.63